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## A PRELIMINARY SURVEY OF THE SOIL FAUNA OF AGRICULTURAL LAND

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### (I) INTRODUCTION.

It is widely recognised that cultivation has some detrimental effect upon the soil fauna, and various cultural operations are strongly advocated as preventive and remedial measures against the depredations of soil insects. However, it is not known whether arable land possesses a characteristic fauna apart from species peculiar to certain crops, or whether certain species, taking grassland as being the immediate initial condition, are eliminated by cultivation.

Hence it was considered that a survey of the fauna of agricultural land, both arable and grass, might lead to some conclusions as to the effect of cultivation.

A survey is generally attempted either as a piece of taxonomic work or as an ecological investigation. The taxonomic method has become unpopular since it is an inadequate expression of the work, for all the observation and detail obtained end merely in a classified list of names. At the same time the rise of Ecology has tended to change the view-point.

Ecology, treating of the general life processes of the animal as opposed to the physiology of organs, has provided an attractive alternative. Unfortunately, however, the subject of Animal Ecology has received

little attention, apart from the valuable work of a small number of investigators. In America something has been done to formulate the principles and methods of animal ecology by Adams, Forbes, Shelford, Vestal and others. In this country almost the only serious attempt at this problem is due to Cameron. The present paper is an endeavour to extend his investigations on soil-insects from grassland to other types of agricultural land.

It is by no means easy to find the distribution in space of the association if the definition of Forbes is accepted (1907).

Cameron has suggested (1916) that a difference in the fauna of two areas possessing different soil-types and vegetative coverings is due to different environmental conditions.

The fauna in an area may exist, however, without any ecological connection between the different species. They may not form an association. If the fauna in two areas come together without any ecological relationship (*i.e.* by chance) it is not possible to state in what degree environmental conditions operate since this chance occurrence may take place under very diverse environmental conditions. Even if an association occurs it may be largely composed of areas of associated species without any ecological connections. There may be also environmental differences within the association allowing of the presence of a different type of fauna. At the same time the species most frequently found seem to occur irrespective of soil-type and the majority of species, being adapted to general feeding, are not restricted to particular plant species or vegetative covering.

If the definition of the association is followed it seems that it operates over broad tracts of country comparable with climatic regions, thus, to the isolated worker to whom the investigation of more than a strictly limited area is impossible, the association has a theoretical rather than a practical value, and it therefore becomes necessary to find some smaller or more practical basis for his research methods.

An attempt therefore has been made in this investigation to standardise the soil-types as far as possible. If instead of taking an area with a varied number of soil-materials, one soil-type is used, more accurate information can be obtained as to the physical condition of the soil, water-content and aeration. In this way the environmental conditions may be expressed to some extent in terms of the soil-type. It is felt that if the results from a number of individual surveys are linked together to cover large areas the solution to the whole problem may be found.

(II) THE SURVEY.

In the conduct of the survey while too much attention cannot be paid to correct soil-sampling, there is entailed something more than the close examination of soil-samples in the laboratory. It is essential in tracing the influence of cultivation to study the survey areas under every weather condition and especially both during and immediately after cultural operations.

In considering suitable localities for the survey areas regard had to be paid to the desirability of the stations selected being at such a distance from the industrial towns as to lessen, to some extent, the effects due to atmospheric impurities; and at the same time to make sure that the fields chosen should be representative of the soil-type in each district.

The survey was carried out on three types of agricultural land.

(a) Land continuously under the plough for a number of years.

(b) Pasture land, which had been broken up not less than three years previous to the survey. This interval of time was decided upon in order that the life-histories of most of the species present would have been completed at least once, and any effects upon the fauna, which cultivation might possess, would have come into full play after that space of time.

(c) Permanent pasture or meadowland providing a "control" to the conditions on arable land and giving some indication as to seasonal variation in the environment.

No. 1 Station, Haveley Hey, is situated  $1\frac{3}{4}$  miles south-west of Northenden, Cheshire. The geological formation is the Lower Keuper Sandstone or Waterstones overspread by Drift, composed of sand, gravel and reddish clay with boulders.

The district has an altitude of about 175 feet, and lies comparatively close to the southern bank of the River Mersey. In fact, the height of the river during floods is indicated by the excessive rising of the water-table in the fields, due to the inability of the water to flow away through the drains. The neighbourhood is comparatively open country, but there are a number of small woods scattered over the area.

The Field A ("Moat Field," Haveley Hey Farm, Northenden), chosen as an example of arable land, has been continuously under the plough for many years and is a typical arable soil of that district. The field itself is fairly level, but on the west side slopes down into a hollow in which runs a small stream.

The rotation of crops is as follows: (1) Clover, 1916; (2) second year

ley, 1917; (3) Oats, 1918; (4) Potatoes, Turnips and Mangels, 1919; (5) Wheat, 1920.

The investigation was commenced in October 1919, when the root crop had just been taken from the ground, and the land was in its cleanest condition.

The field received an autumn ploughing at the end of November and beginning of December. The land is a heavy loam and works rather stiffly under the plough on account of the unusually large proportion of the finer fractions of silt and clay. Thus there was a tendency for the soil particles to run together to form hard clods in wet weather.

No farmyard manure was applied to the land previous to ploughing since the wheat followed a root crop. But in the spring of 1919 a heavy dressing of farmyard manure was given preparatory to the root crop. Artificial manures as a top-dressing for wheat were not used, so that any manurial effect upon the soil fauna is due to the farmyard manure alone.

At the beginning of February the wheat seed was drilled without any preparatory harrowing. The field was harrowed to cover the seed, and during the spring the wheat was rolled and harrowed.

To summarise, it will be understood that the minimum of working was done to the land consistent with the proper cultivation of the crop. Any immediate influence which cultivation has had upon the soil fauna is due to the exposing of the surface layer of soil by the autumn ploughing and the working during the early part of the year. Also any indirect effect will be caused by the residues of former crops and of farmyard manure, the accumulation of weeds and fauna introduced by reason of the growth of previous crops in the rotation.

No. 2 Station, Brandlesholme, lies about  $2\frac{1}{4}$  miles north-west of the town of Bury, Lancashire. The district is situated upon the Coalmeasures, overlain by Drift consisting of upper sand and gravel.

Brandlesholme forms an elevated tableland about 420 feet above sea-level. On the east lies the River Irwell, to which the land slopes sharply. On the west it declines again to form a hollow in which runs Kirklees Brook. Surrounding the district on all sides, except the south where the town of Bury is situated, are high hills running up into the Pennine Chain. Thus the situation of No. 2 Station is rather exposed.

Two fields were taken as types of arable land ("broken-up" pasture and permanent pasture). These were respectively "Bung's Field" and "Big Meadow" (Brandlesholme Hall Farm, Bury).

Field B ("Bung's Field") was pasture ploughed up in the autumn of 1916 in accordance with the "Ploughing-up Programme" (War-time

legislation). There is a slight elevation in the middle line and the field slopes very gradually to the eastern and western sides.

No regular rotation has been followed upon this field, but the following crops have occupied the land: (1) Potatoes and Turnips, 1917; (2) Oats and Vetches, 1918; (3) Seeds, 1919; (4) second year ley, 1920.

Previous to the commencement of the investigation in October 1919 the "aftermath" of the "seeds" was mown at the end of August 1919. During the winter and spring the land received no treatment beyond the application of a dressing of farmyard manure (10 tons per acre) at the beginning of December.

Unlike Field A, the land surrounding Field B is mostly under grass and not a mixed tenure of corn and grass land.

The soil is a light to medium loam. There is a great abundance of water in this district, but the water content of the soil does not appear to affect its mechanical condition seriously, probably owing to the large amount of coarse sand present.

The effect of cultivation upon the soil fauna in this case does not seem to be so drastic as with Field A. Any direct influence of cultural operations is absent apart from the application of the manure.

Field C ("Big Meadow") consists of permanent pasture or meadowland. The field falls away gently towards the south. There are a number of large ponds or mill reservoirs lying on its western side between the field and the stream in the hollow. There is much water present. At almost the highest elevation the water-supply to the farm is maintained by a wind-engine pumping from a 15 feet well, the greater amount of water flowing in from the upper layers of soil.

As with Field B the surrounding land is under grass. Strictly speaking this land is a meadow since it is mown annually for hay. Haymaking takes place at the end of June. During the winter a dressing of farmyard manure was applied as in the case of Field B. With the exception of "chain-harrowing" in the spring there was no further cultural operations.

Apart from the change in the botanical composition induced by annually mowing the field, it may be considered that Field C is a typical pasture or meadowland and that the same influence upon the soil fauna, found in general to operate in other pastures, will be present.

The investigation of the different areas was carried out from October to May 1919-20. Although it would be desirable that the survey should cover a complete year, there is a certain advantage in practice in making the investigation at that time of the year. Conditions on the whole are much more stable. There is not that constant migration from subter-

anean and field strata to aerial stratum which takes place during the summer months. Most species of soil-insects are hibernating in the larval or pupal form and the other fauna experience a condition of diminished activity.

In order that a more exact idea might be obtained with regard to the soil conditions, a mechanical analysis was carried out:

| Fractions                                  | Diameter of particles | A<br>Moat Field<br>% | B<br>Bung's Field<br>% | C<br>Big Meadow<br>% |
|--------------------------------------------|-----------------------|----------------------|------------------------|----------------------|
| Fine gravel                                | 1-3 mm.               | 2.77                 | 1.69                   | 3.50                 |
| Coarse sand                                | 0.2-1 mm.             | 20.55                | 44.30                  | 56.40                |
| Fine sand                                  | 0.04-0.2 mm.          | 28.83                | 17.55                  | 10.33                |
| Silt                                       | 0.01-0.04 mm.         | 11.78                | 6.19                   | 3.56                 |
| Fine silt                                  | 0.002-0.01 mm.        | 15.64                | 6.50                   | 3.03                 |
| Clay                                       | less than 0.002 mm.   | 12.29                | 8.19                   | 8.29                 |
| Soluble matter and<br>Hygroscopic moisture | —                     | 6.67                 | 10.11                  | 12.98                |

Soil-samples of a standard size in lines across the field were taken so that representative samples might be obtained. The 9-inch cube sample was used because 9 inches deep is usually the limit of habitable soil, few species being found below that depth and at 9 inches the soil passes into subsoil on most agricultural land.

After taking the sample, the soil was spread out and allowed to dry in the laboratory for two days. It was treated with three sieves of  $\frac{1}{4}$  inch,  $\frac{1}{8}$  inch and 1 mm. While sifting, the soil both in the sieve and that which had passed through was constantly examined for any specimens. With practice two siftings are sufficient to detect all species, but some dipterous larvae managed to pass the 1 mm. sieve. Little difficulty was experienced by this method in noticing any specimens which feigning death, remained still and harmonised with the soil, because the action of the sifting seemed to bewilder and prevent them remaining motionless.

The specimens were preserved in 5 per cent. formalin, but Dipterous and Coleopterous larvae and pupae were previously boiled. Larvae and pupae, especially those belonging to the Diptera, which could not be immediately identified, were placed in breeding cages in order that the adult form might be obtained.

Special difficulties were encountered in sampling. It was found desirable to let samples dry for a few days since their moist condition in the fresh state prevented effective sifting. Owing to the clayey nature of the Northenden soil it was impossible to take samples in wet weather because the mechanical condition was such as to form hard clods impossible to examine.

## (III) THE EFFECT OF CULTIVATION.

In studying the effect of cultivation upon the soil fauna, a comparison of that of grass and arable land in similar areas will be of value, since it may be taken that grassland is the immediate initial condition and that differences demonstrated on arable land are due to environmental conditions induced by cultural operations. It will be seen from an examination of the lists of species attached to this paper that such a comparison leads to several definite conclusions.

(1) The distribution and numbers of the soil fauna are more stable on grass than on arable land. Grassland bears a vegetative covering through a period when little, if any, vegetation exists on arable land. Consequently food material is always present for the large majority of species, since soil fauna are predominantly phytophagous forms. At the same time the land is not cultivated and the hibernation of species or period of lessened activity proceeds normally. On arable land, the opposite is the case, the winter ploughing and working of the soil brings the fauna to the surface and exposes the animal life not only to the harsh climatic conditions but also to bird attack.

(2) There is a corresponding increase in the fauna on both arable and grassland as vegetative growth increases. This circumstance is to be expected since conditions favourable to plants are those most suited to animal life. That this increase does take place on arable land is shown either by the absence or great scarcity of species from the earlier samples taken in winter. It will be understood that the conditions in winter and early spring are extremely detrimental to soil fauna. At that time all circumstances combine to reduce animal life in a drastic manner on arable soil.

It may be said that the fauna of arable land consists of (a) Species which have existed from the previous year by passing the winter in the soil; (b) Species which are introduced or migrate there in the growing season.

With regard to the first class the survey has shown that at a time when the wintering species were alone in occupation few are obtained in the samples.

The fact that the increase of numbers on arable land always lags behind the increase on grassland, rather indicates that grassland is the source of the influx of fauna on arable land in the growing season. Of course certain species will be attracted to the particular crop and may form the dominant ones for that year. With regard to those commonly occurring it does not seem that their limited numbers on grassland are

sufficient to cause a strenuous competition for food and consequent migration of members of species to less populated areas, such as arable land. The invading species will have at the same time to face the more unsuitable environmental conditions found on arable soil. Accidental migration will take place but will hardly provide an adequate explanation.

(3) There is no characteristic fauna of arable land. The predominant species on arable are those commonly found on pasture. It is not possible in an investigation where only a limited number of species are obtained, to discover whether any of them are particularly susceptible to cultural operations and are eliminated either directly or by deprivation of food material. Even where the absence of some commonly occurring species is shown on arable land the environmental conditions as a whole rather than cultivation as such may provide the true explanation.

It will be understood that owing to the particular nature and uniformity of the vegetation on arable land different species will predominate from year to year. These, however, cannot be considered to form a special fauna since the effect is due to the overwhelming importance of perhaps one factor in the environment, such as the particular crop grown.

The great disadvantage in taking samples to determine the population of an area is that a large error either way must be allowed for in the computation. The tendency in sampling is that dominant species are stressed, and rarer species, since they may occur only in a certain particular section of the area, may be overlooked. The elimination of species by cultivation can only be determined by the comparison of the results from a large number of separate surveys.

I am indebted to Professor S. J. Hickson for the kind interest he has always taken in the work and to Mr R. A. Wardle, M.Sc., Lecturer in Zoology (Manchester University), at whose suggestion the survey was undertaken.

With regard to the classification of soil fauna I have to acknowledge the valuable assistance of Mr H. Britten (Manchester Museum) and the Rev. G. Brade-Burke, M.Sc. (South-Eastern Agricultural College, Wye, Kent).

(IV) SCHEDULES OF SPECIES.

Animal Species.

October 1919—May 1920.

(The separate dates in the case of each field represent different soil-samples taken. Where the dates recorded for different species in the same field are identical, those species have occurred together in the same sample.)

(L)=Larva; (P)=pupa. Where no abbreviation follows the date, the adult form is indicated.)

| Species                            | "Big Meadow"<br>(pasture)          | "Bung's Field"<br>("broken-up"<br>pasture)  | "Moat Field"<br>(arable)                     |
|------------------------------------|------------------------------------|---------------------------------------------|----------------------------------------------|
| <i>Collembola:</i>                 |                                    |                                             |                                              |
| <i>Onychiurus ambulans</i> , L.    | —                                  | Oct. 19th (8)<br>26th<br>Nov. 2nd           | Nov. 5th                                     |
| <i>Coleoptera:</i>                 |                                    |                                             |                                              |
| <i>Notiophilus biguttatus</i> , F. | April 18th                         | May 6th<br>8th (2)<br>12th<br>13th (2)      | May 6th<br>12th<br>14th<br>16th              |
| <i>Leistus rufescens</i> , F.      | May 2nd (L)<br>6th (L)             | —                                           | —                                            |
| <i>L. fulvibarbis</i> , Dej.       | —                                  | Oct. 19th (L)                               | —                                            |
| <i>Nebria brevicollis</i> , F.     | April 4th                          | May 2nd                                     | —                                            |
| <i>Loricera pilicornis</i> , F.    | —                                  | —                                           | May 16th<br>17th<br>18th<br>20th             |
| <i>Pterostichus madidus</i> , F.   | Mar. 7th (L)<br>May 6th (L)        | Feb. 22nd (L)<br>April 30th (L)<br>May 2nd  | May 12th (L)                                 |
| <i>P. vulgaris</i> , L.            | April 18th (L)<br>28th (L)<br>30th | Oct. 12th<br>April 27th (L)<br>29th (L)     | May 10th (L)                                 |
| <i>P. strenuus</i> , Pz.           | —                                  | May 2nd<br>April 30th<br>May 3rd            | May 4th                                      |
| <i>Amara plebeia</i> , Gyll.       | —                                  | —                                           | May 2nd<br>14th<br>16th<br>20th              |
| <i>Anchomenus dorsalis</i> , Mull. | —                                  | —                                           | May 16th                                     |
| <i>A. parum-punctatus</i> , F.     | —                                  | May 10th                                    | —                                            |
| <i>Bembidium littorale</i> , Ol.   | Mar. 7th                           | —                                           | May 10th<br>17th (2)<br>18th<br>19th<br>20th |
| <i>B. obtusum</i> , Stm.           | —                                  | May 8th                                     | —                                            |
| <i>B. quadrimaculatum</i> , L.     | —                                  | —                                           | May 18th                                     |
| <i>B. guttula</i> , F.             | —                                  | —                                           | May 19th<br>20th                             |
| <i>B. lampros</i> , Hbst.          | —                                  | May 8th (3)<br>10th (2)<br>12th (3)<br>13th | —                                            |
| <i>Tachyporus pusillus</i> , Gr    | Jan. 4th                           | —                                           | —                                            |
| <i>Ocypus cupreus</i> , Rossi      | May 2nd                            | —                                           | —                                            |
| <i>Philonthus varius</i> , Gyll.   | April 18th                         | —                                           | —                                            |
| <i>Xantholinus linearis</i> , Ol.  | Feb. 22nd (L)                      | —                                           | Nov. 29th (L)                                |
| <i>Aphodius fimetarius</i> , L.    | Feb. 22nd (2L)<br>April 18th (L)   | —                                           | —                                            |

| Species                                                   | "Big Meadow"<br>(pasture) | "Bung's Field"<br>("broken-up"<br>pasture) | "Moat Field"<br>(arable) |
|-----------------------------------------------------------|---------------------------|--------------------------------------------|--------------------------|
| <i>A. prodromus</i> , Brahm.                              | —                         | —                                          | May 12th                 |
| <i>Geotrope stercorarius</i> , L.                         | May 10th                  | —                                          | —                        |
| <i>Cryptohypnus riparius</i> , F.                         | Jan. 4th                  | —                                          | May 16th                 |
| <i>Agriotes obscurus</i> , L.                             | Jan. 4th (L)              | Oct. 12th                                  | May 1st (2L)             |
|                                                           | Mar. 28th (L)             | April 29th (L)                             | 2nd (L)                  |
|                                                           |                           |                                            | 3rd (L)                  |
|                                                           |                           |                                            | 4th (L)                  |
|                                                           |                           |                                            | 6th (L)                  |
|                                                           |                           |                                            | 8th (L)                  |
|                                                           |                           |                                            | 10th (L)                 |
|                                                           |                           |                                            | 12th (2L)                |
|                                                           |                           |                                            | 14th (L)                 |
|                                                           |                           |                                            | 16th                     |
|                                                           |                           |                                            | 18th (L)                 |
| <i>Athous haemorrhoidalis</i> , F.                        | Jan. 4th (L)              | Oct. 12th (L)                              | May 8th (L)              |
|                                                           | Mar. 28th (L)             | Feb. 22nd (L)                              |                          |
|                                                           | May 10th (L)              | May 6th (2L)                               |                          |
|                                                           |                           | 8th (L)                                    |                          |
| <i>Athous</i> sp.                                         | —                         | —                                          | May 12th (3L)            |
| <i>Corymbites pectinicornis</i> , L.                      | Feb. 22nd (L)             | May 2nd (L)                                | —                        |
|                                                           | Mar. 28th (L)             | 3rd (L)                                    |                          |
| <i>C. cupreus</i> , F.                                    | May 2nd                   | —                                          | —                        |
| <i>Campylus linearis</i> , L.                             | —                         | Oct. 26th (L)                              | —                        |
|                                                           |                           | Jan. 18th (L)                              |                          |
| <i>Phyllobius pyri</i> , L.                               | April 30th (p)            | —                                          | —                        |
|                                                           | May 2nd                   |                                            |                          |
| <i>Harpalus aeneus</i> , F.                               | —                         | May 8th                                    | —                        |
|                                                           |                           | 11th                                       |                          |
|                                                           |                           | 13th                                       |                          |
| <i>Phaedon tumidulus</i> , Germ.                          | —                         | —                                          | May 12th                 |
| <i>Apion violaceum</i> , Kirby                            | —                         | —                                          | May 18th                 |
| <i>Lathrobium fulvipenne</i> , Gr.                        | —                         | —                                          | May 8th                  |
| <i>Diptera:</i>                                           |                           |                                            |                          |
| <i>Empis borealis</i> , L.                                | April 4th (L)             | —                                          | —                        |
| <i>Empis</i> sp.                                          | April 23rd (L)            | —                                          | —                        |
| <i>Onesia sepulchralis</i> , L.                           | April 23rd (L)            | —                                          | —                        |
| <i>Leptis scolopacea</i> , L.                             | April 23rd (p)            | —                                          | —                        |
| <i>Bibio Johannis</i> , L.                                | May 2nd (3)               | —                                          | —                        |
| <i>Tipula</i> sp.                                         | Feb. 22nd (2L)            | Feb. 29th (L)                              | May 2nd (L)              |
|                                                           | 29th (5L)                 | Mar. 7th                                   | 4th (L)                  |
|                                                           | Mar. 7th (L)              | April 4th (L)                              | 8th (L)                  |
|                                                           | 21st (L)                  | 23rd                                       | 14th (L)                 |
|                                                           | April 4th (3L)            | 25th (L)                                   | 16th (L)                 |
|                                                           | 15th (L)                  | 27th (L)                                   | 17th (L)                 |
|                                                           | 18th (L)                  | 29th (L)                                   | 20th (L)                 |
|                                                           |                           | 30th (L)                                   |                          |
|                                                           |                           | May 6th (L)                                |                          |
|                                                           |                           | 12th (L)                                   |                          |
| <i>Hymenoptera:</i>                                       |                           |                                            |                          |
| <i>Dolerus haematodes</i> , Schr.                         | May 2nd (L)               | —                                          | —                        |
| <i>Myrmica laevinodis</i> , Nylander                      | —                         | May 6th (3)                                | —                        |
| <i>Chilopoda and Diplopoda:</i>                           |                           |                                            |                          |
| <i>Lithobius forficatus</i> , L.                          | April 18th                | —                                          | —                        |
| <i>Brachygeophilus truncorum</i> ,<br>Bergsøe et Meinert. | April 25th                | Oct. 26th                                  | —                        |
| <i>Geophilus electricus</i> , L.                          | —                         | —                                          | Feb. 25th                |
| <i>G. insculptus</i> , Attenis                            | Mar. 28th                 | —                                          | —                        |
| <i>Acarina:</i>                                           |                           |                                            |                          |
| <i>Pergamasus crassipes</i>                               | —                         | Oct. 19th                                  | —                        |

**Plant Species.**

*"Big Meadow" (Pasture). (Dominant Species.)*

*Anthoxanthum odoratum*, L., *Alopecurus pratensis*, L., *Phleum pratense*, L., *Agrostis alba*, L., *Agrostis vulgaris*, L., *Holcus lanatus*, L., *Cynosurus cristatus*, L., *Dactylis glomerata*, L., *Poa annua*, L., *Poa pratensis*, L., *Poa trivialis*, L., *Festuca pratensis*, L., *Bromus mollis*, L., *Lolium perenne*, L., *Ranunculus acris*, L., *Bellis perennis*, L., *Taraxacum dens-leonis*, Dest., *Trifolium pratense*, L.

*"Bung's Field" (Broken-up Pasture).*

*Crop—"Seeds" (second year ley):* *Lolium italicum*, A. Br.

*Dominant weeds:* *Stellaria media*, Vill., *Bellis perennis*, L., *Taraxacum dens-leonis*, Dest., *Ranunculus repens*, L., *Spergula arvensis*, L., *Senecio vulgaris*, L., *Plantago major*, L.

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ON FORMS OF THE HOP (*HUMULUS LUPULUS* L.)  
RESISTANT TO MILDEW (*SPHAEROTHECA*  
*HUMULI* (DC.) BURR.); V<sup>1</sup>

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*Seedlings raised at Wye from seed of the "wild hop"*  
(*H. Lupulus* L.) obtained from Vittorio, Italy.

IN previous articles<sup>2</sup> it has been recorded that certain seedling hop-plants of the origin given above are resistant to the attacks of the mildew *Sphaerotheca Humuli* (DC.) Burr. The further observations made during the season of 1920, and recorded below, bring the investigations, which have been continued through seven seasons (1914-1920) to a close. The facts observed during 1920 will be given first, and then a general summary of the results obtained since the investigations were started in 1914.

*Observations made during the season 1920.*

Cuttings of certain seedlings of the "wild hop" from Italy were grown in pots in the greenhouse and tested for resistance to mildew under the conditions described in previous experiments.

The following table gives a list of these seedlings, together with the number of cuttings ("clone-plants") used.

Not one of these 200 plants, raised vegetatively from 23 different seedlings, showed a trace of mildew on any part throughout the growing season, although inoculated with *conidia* both artificially on several occasions, and naturally almost continuously by currents of air carrying *conidia* from several hundred mildewed hop-plants closely surrounding them.

Some of the hop-plants surrounding them were cuttings of other seedlings of the same origin as the 23 "immune" seedlings noted above.

<sup>1</sup> A grant in aid of publication has been received for this communication.

<sup>2</sup> See *Annals of Applied Biology*, vi, 293-310 (1920), where a complete Bibliography is given.

Table I.

*List of Seedlings showing Immunity to Mildew, in the greenhouse, throughout the season of 1920.*

| Ref. no. of seedling | No. of clone-plants | Ref. no. of seedling | No. of clone-plants |
|----------------------|---------------------|----------------------|---------------------|
| V 91                 | 6                   | OA 49                | 7                   |
| V 92                 | 6                   | OB 34                | 32                  |
| V 93                 | 14                  | OD 19                | 9                   |
| Z 2                  | 10                  | OR 38                | 28                  |
| Z 14                 | 10                  | OR 39                | 27                  |
| Z 17                 | 5                   | OY 18                | 1                   |
| <sup>1</sup> Z 20    | 2                   | <sup>1</sup> HH 20   | 2                   |
| Z 22                 | 8                   | HH 44                | 5                   |
| Z 25                 | 10                  | <sup>1</sup> II 13   | 2                   |
| Z 31                 | 1                   | II 24                | 2                   |
| Z 42                 | 9                   | II 30                | 2                   |
| OA 34                | 2                   |                      |                     |
| Total . . . . .      |                     | 200                  |                     |

In both cases the cuttings had been potted up in the same kind of soil and grown under the same conditions. The former plants, however, became naturally infected with mildew by *conidia* disseminated in the air of the greenhouse. In those cases where an asterisk is placed in the table given below, the seedling showed extreme susceptibility; in the other cases the susceptibility shown was normal<sup>2</sup>.

Table II.

*List of Seedlings (of the same origin as in Table I) showing Susceptibility to Mildew, in the greenhouse, throughout the season of 1920.*

| Ref. no. of seedling | No. of clone-plants | Ref. no. of seedling | No. of clone-plants |
|----------------------|---------------------|----------------------|---------------------|
| *Z 24                | 8                   | OA 35                | 2                   |
| *Z 26                | 9                   | OA 36                | 1                   |
| Z 39                 | 8                   | OA 53                | 1                   |
| *Z 41                | 9                   | *OB 48               | 1                   |
| Z 54                 | 2                   | OD 16                | 1                   |
| OA 25                | 3                   | *OD 18               | 4                   |
| *OA 26               | 3                   | II 31                | 1                   |
| Total . . . . .      |                     | 53                   |                     |

<sup>1</sup> These seedlings had not previously been tested; the remaining 20 seedlings had shown the same resistance in previous seasons.

<sup>2</sup> As further evidence of the severity of the inoculation to which the "immune" seedlings were exposed, and of the presence of suitable conditions for the growth of the mildew, it may be mentioned that 63 cuttings of various commercial varieties of hops stood in the same greenhouse and that all these became naturally infected within three weeks.

All the above 53 "clone-plants"—cuttings taken from 14 seedlings—became fully infected, and the mildew persisted on them until the end of the growing season.

The cuttings of both the "immune" and "susceptible" seedlings enumerated above were all taken from the parent-plants, growing in the Experimental Hop-garden at Wye College, in the winters of 1917, 1918 or 1919. In those cases where cuttings were taken in successive years, no change from immunity to susceptibility, or *vice versâ*, was ever found. The 200 immune plants mixed in among the other seedlings (of the same origin) white with mildew afforded the most convincing proof of the different "constitutional" characters possessed by seedlings of a wild plant. In many cases, *e.g.* with the cuttings of Z 24, Z 26, Z 41, OA 35, OD 18, II 31, the "susceptible" parent-plant has been grown in the hop-garden by the side, and within  $3\frac{1}{2}$  feet, of the "immune" parents (Z 25, Z 42, OA 34, OD 19, II 30), so that all these parent-plants have thus been subjected to exactly the same soil, cultural, manurial and weather conditions. It is clear that the differences in susceptibility shown are inherent in the particular seedlings and not induced by any special environmental conditions.

The phenomenon of "semi-immunity"<sup>1</sup> was again shown by a few seedlings when exposed to infection in the greenhouse. The details are given below.

Table III.

*List of Seedlings (of the same origin as in Tables I and II) showing "semi-immunity," in the greenhouse, throughout the season of 1920.*

| Ref. no. of seedling              | No. of clone-plants |
|-----------------------------------|---------------------|
| Z 15 (semi-immune)                | 2                   |
| Z 23       "                      | 4                   |
| Z 38       "                      | 1                   |
| OC 6       "                      | 4                   |
| BB 5       "                      | 1                   |
| OA 33 (approaching semi-immunity) | 4                   |
| OD 17       "       "             | 4                   |
|                                   | <hr/> 20            |

The seedling Z 38 had not before been tested in the greenhouse; the other seedlings had shown "semi-immunity" in previous seasons.

A *résumé* may now be given of the facts observed from 1914 to 1920 as to the susceptibility to mildew of the seedlings of the wild hop. From

<sup>1</sup> Described in *Annals Appl. Biology*, vi, 302 (1920).

1914 onwards 480 seedlings have been kept under observation, first as 1- or 2-year-old seedling plants in the greenhouse, and secondly as older, flowering plants planted out in the Experimental Hop-garden at Wye College, where they have been cultivated (trained, "cut," etc.) and manured according to the usual practice in a commercial hop-garden<sup>1</sup>. In the greenhouse the plants were subjected to the severest test by being inoculated naturally almost continuously with *conidia* from surrounding heavily-infected plants, as well as being occasionally artificially inoculated, with the result that, except for the seedlings noted below, they all became severely infected with mildew. In the Hop-garden natural inoculation was relied upon (except in one experiment) to test the degree of susceptibility of the mature plant. Under the conditions prevailing, this method was found to be satisfactory. Mildew was present generally in the hop-garden (at the time when observations were made on the seedlings) in each season from 1916 to 1920, and particularly severe outbreaks of mildew occurred in 1916, 1919 and 1920. Owing to the late-flowering habit of the wild hop, and consequent prolonged period of growth, it was found that October was the best month for examination as to the incidence of mildew. In the case of the ♀ plant, the production at the end of August and during September of the female inflorescence ("burr") and young developing hops provided the best possible infectible material. With the most susceptible seedlings the attacks were so severe that season after season the greater proportion of the "hops" (cones) were deformed by the mildew, or not infrequently the crop of "hops" was entirely destroyed, the female inflorescences being permanently arrested in development and changed into white, hypertrophied, knob-like growths. With the ♂ plant, the infectible material consisted for the most part of the leaves of the axillary side-shoots which developed during late-summer from the lower portion of the main stem ("bine"); where vigorous side-shoots were produced, these provided excellent infectible material, but in those cases where they were absent, as happened with a few plants in certain seasons when they "ripened off" early, the susceptibility could not be ascertained. With very susceptible seedlings, branches of the male inflorescence sometimes became mildewed.

In view of the impossibility of recording in detail the behaviour of all the 480 seedlings, a selection has been made of 52 seedlings, whose records are given in Table IV. The explanations of the signs used are as

<sup>1</sup> Owing to exigencies of space, the seedlings could not be planted all together, but had to be placed, usually in large blocks, but sometimes singly, throughout the Experimental Hop-garden of 2½ acres.

Table IV.

| Ref. no. | Sex                                              | 1916           |   | 1917           |   | 1918           |    | 1919           |    | 1920                             |    |
|----------|--------------------------------------------------|----------------|---|----------------|---|----------------|----|----------------|----|----------------------------------|----|
|          |                                                  | H              | G | H              | G | H              | G  | H              | G  | H                                | G  |
| V 91     | O <sub>3</sub> O <sub>3</sub> O <sub>3</sub> + O | —              | O | —              | O | S <sup>1</sup> | —  | O              | O  | O                                | O  |
| V 92     |                                                  | —              | O | —              | O | S <sup>1</sup> | —  | O              | O  | O                                | O  |
| V 93     |                                                  | —              | O | —              | O | S <sup>1</sup> | —  | S <sup>1</sup> | O  | O                                | O  |
| Z 1      |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sub>2</sub> | —  | S <sup>1</sup>                   | —  |
| Z 2      |                                                  | —              | — | O              | O | O              | O  | O              | O  | O                                | O  |
| Z 14     |                                                  | —              | — | O              | — | S <sub>2</sub> | —  | O              | O  | S <sup>1</sup>                   | —  |
| Z 15     |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | ½S | S <sub>2</sub> | ½S | ½S                               | ½S |
| Z 16     |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | —              | —  | —                                | —  |
| Z 17     |                                                  | —              | — | O              | — | —              | —  | O              | —  | —                                | O  |
| Z 19     |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sub>2</sub> | —  | S <sup>2</sup>                   | —  |
| Z 20     |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | O              | —  | S <sup>1</sup> or S <sup>2</sup> | O  |
| Z 22     |                                                  | —              | — | O              | — | S <sub>2</sub> | O  | O              | O  | S <sup>1</sup> or S <sup>2</sup> | O  |
| Z 23     |                                                  | —              | — | S <sub>2</sub> | — | O              | ½S | S <sup>1</sup> | ½S | —                                | ½S |
| Z 24     |                                                  | S <sub>2</sub> | — | S <sub>2</sub> | — | S <sup>2</sup> | S  | S <sub>2</sub> | S  | —                                | S* |
| Z 25     |                                                  | O              | — | O              | — | O              | O  | O              | O  | S <sup>1</sup>                   | O  |
| Z 26     |                                                  | S <sub>2</sub> | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sub>2</sub> | S  | S <sup>2</sup>                   | S* |
| Z 31     |                                                  | —              | — | —              | — | S <sub>2</sub> | —  | S <sup>1</sup> | O  | —                                | O  |
| Z 38     |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | O              | —  | —                                | ½S |
| Z 39     |                                                  | —              | — | S <sub>2</sub> | S | S <sup>2</sup> | S  | S <sub>2</sub> | —  | —                                | ½S |
| Z 41     |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sub>2</sub> | S* | S <sup>2</sup>                   | S* |
| Z 42     |                                                  | —              | — | O              | — | O              | O  | —              | O  | —                                | O  |
| Z 43     |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sup>1</sup> | —  | S <sup>2</sup>                   | —  |
| Z 54     |                                                  | —              | — | S <sub>2</sub> | S | S <sub>2</sub> | —  | S <sub>2</sub> | —  | —                                | S  |
| OA 25    |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sup>1</sup> | —  | S <sup>1</sup>                   | S  |
| OA 26    |                                                  | —              | — | S <sub>2</sub> | — | S <sup>2</sup> | —  | S <sup>2</sup> | S* | S <sup>2</sup>                   | S* |
| OA 33    |                                                  | —              | — | O              | — | O              | ½S | S <sub>2</sub> | ½S | S <sup>1</sup>                   | ½S |
| OA 34    |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sup>1</sup> | —  | S <sup>1</sup>                   | O  |
| OA 35    |                                                  | —              | — | S <sub>2</sub> | — | S <sup>2</sup> | —  | S <sup>2</sup> | S  | S <sup>2</sup>                   | S  |
| OA 36    |                                                  | —              | — | S <sub>2</sub> | — | S <sub>2</sub> | —  | S <sup>2</sup> | S  | S <sup>2</sup>                   | S  |
| OA 49    |                                                  | —              | — | O              | — | O              | O  | O              | O  | S <sup>1</sup>                   | O  |
| OB 26    |                                                  | —              | O | —              | O | —              | O  | —              | —  | —                                | —  |
| OB 34    |                                                  | —              | — | O              | — | S <sup>1</sup> | O  | —              | O  | O                                | O  |
| OB 48    |                                                  | —              | — | S <sub>2</sub> | — | S <sup>2</sup> | —  | S              | S  | S <sup>2</sup>                   | S* |
| OC 6     |                                                  | —              | — | O              | — | O              | ½S | S <sup>1</sup> | ½S | S <sup>2</sup>                   | ½S |
| OD 16    |                                                  | —              | — | S <sub>2</sub> | — | S <sup>2</sup> | —  | S <sub>2</sub> | S  | S <sup>2</sup>                   | S  |
| OD 17    |                                                  | —              | — | S <sub>2</sub> | — | S <sup>1</sup> | —  | S <sup>1</sup> | —  | S <sup>1</sup>                   | ½S |
| OD 18    |                                                  | —              | — | S <sub>2</sub> | — | S <sup>2</sup> | —  | S <sub>2</sub> | —  | S <sup>2</sup>                   | S* |
| OD 19    |                                                  | —              | — | O              | — | O              | O  | S <sup>1</sup> | O  | S <sup>1</sup>                   | O  |
| OE 14    |                                                  | —              | O | —              | O | —              | O  | —              | —  | S <sup>1</sup>                   | —  |
| OR 38    |                                                  | S <sup>1</sup> | — | S <sub>2</sub> | O | S <sub>2</sub> | O  | S <sup>1</sup> | O  | S <sub>2</sub>                   | O  |
| OR 39    |                                                  | S <sup>1</sup> | — | —              | O | O              | O  | O              | O  | O                                | O  |
| OY 18    |                                                  | —              | — | —              | — | O              | —  | S <sup>1</sup> | O  | O                                | O  |
| BB 5     |                                                  | —              | — | —              | — | S <sup>1</sup> | —  | O              | —  | —                                | —  |
| DD 31    |                                                  | —              | O | —              | O | —              | O  | S <sup>1</sup> | —  | —                                | —  |
| HH 20    |                                                  | —              | — | —              | — | S <sup>1</sup> | —  | —              | O  | —                                | O  |
| HH 44    |                                                  | —              | — | S <sup>1</sup> | — | S <sup>1</sup> | O  | S <sup>1</sup> | O  | —                                | O  |
| II 11    |                                                  | —              | — | —              | — | S <sup>1</sup> | —  | —              | S  | —                                | S  |
| II 13    |                                                  | —              | — | —              | — | S <sup>1</sup> | —  | —              | O  | —                                | O  |
| II 24    |                                                  | —              | — | —              | — | O              | —  | O              | O  | —                                | O  |
| II 30    |                                                  | —              | — | —              | — | O              | —  | —              | O  | —                                | O  |
| II 31    |                                                  | —              | — | —              | — | S <sub>2</sub> | —  | —              | —  | —                                | S  |
| 316      | O <sub>3</sub>                                   | —              | O | —              | O | —              | O  | S <sup>1</sup> | —  | S <sup>1</sup>                   | —  |

¶ On Aug. 7 a few small patches of mildew appeared on a few of the young leaves after a spell of abnormally cold, dull weather; these patches soon died away and in October the plant was entirely free from mildew.

follows: H and G indicate respectively that the plant was growing either in the hop-garden or, in a pot, in the greenhouse. O signifies that the plant remained absolutely free from mildew on any part of it throughout the season. — indicates either that the plant was absent, or that no record exists—sometimes because no observations were made or more commonly because no infectible material (with ♂ seedlings in the hop-garden) occurred. It was not found possible, as a rule, to estimate the degree of susceptibility shown in the greenhouse; the letter S stands for “normal” or “full” susceptibility; in a few cases, marked S\*, the plant became so virulently infected, that extreme susceptibility appeared to be indicated. In the hop-garden S<sup>1</sup> indicates that only a minute trace of mildew occurred; S<sup>2</sup> that the infection was of medium intensity; S<sup>3</sup> that the infection was very severe,—those cases where the entire crop of hops was destroyed by mildew being indicated by the added sign †.

The 52 seedlings, whose annual records are given in Table IV, give evidence as to certain facts which will now be discussed.

(a) *Immunity under greenhouse conditions.*

Twenty-seven seedlings have shown persistent immunity to mildew when grown in the greenhouse. The history of the behaviour of these plants in the open, indicated in Table IV, will now be considered in detail. The examination of the plants was made each year in October (see above, p. 149).

Ref. nos. V 91, V 92, V 93. These three seedlings, as soon as raised from the seed, showed complete immunity in the greenhouse throughout the seasons of 1916 and 1917. They were planted out in the hop-garden in November 1917, and in October 1918 all three plants<sup>1</sup> showed a minute trace of mildew, in the case of V 93 consisting of a tiny patch of mildew on the under-surface of one leaf only. In 1919 and 1920 V 91 and V 92 remained free from mildew; V 93 in 1919 had again a tiny “powdery” patch of mildew, at the back of one leaf only, while in 1920 it was free.

Ref. no. Z 2. This seedling was originally planted out in the hop-garden in 1914. Cuttings taken in 1917–18, 1918–19 and 1919–20 proved persistently immune in the greenhouse, and no mildew was observed on the parent-plant in the hop-garden during the years 1917–20, when infectible material was present each autumn, although its neighbour<sup>2</sup>

<sup>1</sup> All three seedlings were then about 5 ft. high and non-flowering.

<sup>2</sup> In every case where reference is made to a neighbouring plant (e.g. Z 16 next to Z 17, Z 24 and Z 26 next to Z 25, and so forth) it is another seedling of the same origin. The seedlings were planted 3 ft. 6 in. apart in the row, and the lateral shoots of neighbouring plants frequently became intertwined.

Z 1 (likewise a ♂ seedling) was infected to the extent of S<sup>2</sup> in 1917, 1918 and 1919, and S<sup>1</sup> in 1920.

Ref. no. Z 14. In the open slight susceptibility was shown in 1918 and 1920; no mildew occurred on the plant in 1917 and 1919, when its neighbour Z 15 became mildewed to the extent of S<sup>2</sup>.

Ref. no. Z 17. In 1917 this seedling remained free from mildew, while Z 16 was mildewed to the extent of S<sup>3</sup>. In other seasons there has been no opportunity of testing Z 17 in the open.

Ref. no. Z 20. This seedling was planted out in 1914; two cuttings taken in 1919–20 proved persistently immune in the greenhouse. In the open the plant was recorded as S<sup>2</sup> in 1917; in 1918 as having a trace of mould on leaves and hops; in 1919 it remained free from mildew, notwithstanding the fact that lateral shoots of Z 19, bearing very mildewed hops, had twined round its stems. In 1920, Z 20 showed a mere trace of mildew on the leaves, but several hops were infected with mildew at the extreme tip—the susceptibility being estimated as being between S<sup>1</sup> and S<sup>2</sup>. There can be no doubt that Z 20 has been severely tested in the open, since its neighbour Z 19 has been smothered in mildew each season and in 1920 had its entire crop destroyed.

Ref. no. Z 22. This seedling remained free from mildew in 1917 (when Z 23 was recorded as S<sup>2</sup>); in 1918 and 1919 the amount of mildew on Z 22 was S<sup>2</sup> on the hops and very occasionally a trace of mildew on the leaves; in 1920 there was a full crop of hops, *i.e.* none was deformed by attacks of mildew, but very occasionally the mildew occurred on the peduncles—the susceptibility being estimated as being between S<sup>1</sup> and S<sup>2</sup>.

Ref. no. Z 25. The history of this seedling is one of the most interesting. It was planted out in the hop-garden in 1914. In 1916 and 1918 it remained free from mildew, although Z 24 and Z 26 on either side of it were smothered with mildew, Z 24 in 1918 having all its hops destroyed by mildew. In June 1918 young leaves of the parent-plants Z 24, Z 25, Z 26 in the open were artificially inoculated with *conidia*; infection resulted on Z 24 and Z 26, while Z 25 proved immune. In 1917 Z 25 remained entirely free from mildew, notwithstanding the fact that several strong lateral shoots of Z 24 had become intertwined with those of Z 25 and had produced very mildewed hops which became intermingled with the “immune” hops of Z 25. In 1919, at the beginning of August, after a spell of abnormally dull, cold weather, a few small patches of mildew occurred on a few of the young leaves of Z 25. These mildew-patches died away completely as the weather became normal (hot and sunny) and no more mildew occurred on the plant. In October

of the same year when the plant was examined minutely all over, no trace of mildew could be found on leaves or hops, although some of the lateral shoots of Z 26, bearing mildewed hops, had twined round the stems of Z 25. In 1920, on August 28, Z 25 was free from mildew; when examined in October there was no mildew on the leaves, but a trace of mildew occurred on the hops, particularly at the tips. In 1920 both Z 24 and Z 26 were so severely infested with mildew that all their hops were destroyed.

Ref. no. Z 31. So far as this seedling has been able to be tested in the open, it shows susceptibility to the extent of S<sup>1</sup>.

Ref. no. Z 42. In the two years, 1917 and 1918, when this seedling could be tested, it remained free from mildew, while Z 41 on one side was S<sup>3</sup>, and Z 43 on the other side was S<sup>2</sup>.

Ref. no. OA 34. In 1917 and 1918 the amount of mildew present (on the hops) was recorded as S<sup>2</sup>; in 1919 and 1920 there was only a mere trace of mildew (also on the hops). The neighbouring plant OA 35 was recorded as S<sup>3</sup> each year, and in 1918, 1919 and 1920 was so severely attacked by mildew that the crop was destroyed.

Ref. no. OA 49. This seedling remained free from mildew in 1917, 1918 and 1919; in 1920 there was a mere trace of mildew on a few hops in an otherwise completely healthy crop. In 1919 a cutting was grown in the greenhouse and proved immune; on July 5 this cutting was taken out of the greenhouse and placed in the open air. The plant produced a fresh shoot, which by September 30 was 1 ft. 8 in. high; round this shoot the stem of another hop-seedling which bore mildewed leaves had twined, but OA 49 remained immune.

Ref. no. OB 26. No opportunity has yet occurred of testing this seedling in the open.

Ref. no. OB 34. The only time that mildew has occurred on this seedling was in October 1918, and then only one "hop" was found infected. This single hop-cone had been attacked when in an early stage of development and had been converted into a knob-like growth (white and powdery with the conidial stage of the mildew). This mildewed "hop" occurred in the midst of a normal crop of healthy hops.

Ref. no. OD 19. This seedling remained free from mildew in 1917 and 1918, notwithstanding the fact that in both seasons OD 18 was mildewed to the extent of S<sup>3</sup>, the crop being destroyed by mildew in 1918. In 1918 a strong lateral shoot of OD 19 climbed round the stem of OD 18 and produced there perfectly healthy hops among the excessively mildewed hops of OD 18. In 1919 OD 19 showed a trace of

mildew—S<sup>1</sup>. In 1920 there was no mildew on the plant on August 31; in October a trace of mildew was found on one hop only.

Ref. no. OE 14. A trace of mildew occurred on the hops in 1920.

Ref. no. OR 38. This seedling appears to be the most susceptible in the open of all the seedlings which show immunity in the greenhouse. As a seedling plant in 1914 it showed persistent immunity in the greenhouse; it was planted out in the hop-garden in 1915. In 1916 its main crop of "hops" was free from mildew, but a late, young stem, which had run up the old stems to nearly the top, bore several leaves and one "hop" with patches of mildew on them. In 1917 there was a fair amount of mildew on the hops (both in the conidial and in the perithecial stages), chiefly on the peduncles but also on the bracts and bracteoles. In 1918, on September 7, there was a fair amount of mildew on the young leaves, and in October, when the whole plant was minutely examined, the hops generally were found to be severely attacked by mildew, a large percentage being undeveloped or deformed through its attacks. In 1919 there was only a trace of mildew on the hops. In 1920 there was a minute trace of mildew on the leaves and an attack of medium intensity on the hops. In the greenhouse OR 38 has been tested on a considerable scale by means of "cuttings" taken in the four winters 1916-1919 from the parent-plant in the hop-garden. In all, 42 "clone-plants" have thus been exposed to constant inoculation in the greenhouse, and with the exceptions noted below, all have proved persistently immune. In 1917 a phenomenon occurred which had not been observed before and which has not been observed since. On two cuttings of OR 38 in the greenhouse, a minute patch of mildew appeared, on one leaf only of each plant—in one case following artificial inoculation, in the other case, without; these mildew-patches appeared in May and soon died away without the mildew spreading on the plant. The two plants concerned, together with three other cuttings of OR 38 stood in the greenhouse for the rest of the season of 1917 and in spite of constant inoculation with *conidia*, all the plants remained persistently immune. It was clear that the phenomenon consisted of the sudden appearance of strictly local and temporary susceptibility (induced by, at present, unknown causes) and was not a general breaking down of the immunity of the plant<sup>1</sup>.

Three cuttings of OR 38 which had remained persistently immune in the greenhouse in 1917, were planted out in the hop-garden in the winter of 1917-18. These three clone-plants of OR 38 have behaved

<sup>1</sup> No other "immune" seedling has ever shown in the greenhouse any signs of breaking down.

as follows. (In 1918 the plants were from  $1\frac{1}{4}$  to 5 ft. high and non-flowering.)

Ref. no. W 56. 1918: A fair amount of mildew ( $S^2$ ) on the leaves. 1919: A trace only of mildew, one hop being destroyed by mildew, and one hop having mildew on the peduncle—otherwise a crop of healthy hops; no mildew on the leaves. 1920: On August 29 there were numerous patches of mildew on three oldish leaves but not elsewhere; in October there was a fair amount of mildew ( $S^2$ ) on the hops.

Ref. no. Y 28. 1918: Very mildewed ( $S^2$ ) on the leaves and stems. 1919: A trace of mildew on two hops only. 1920: At the end of August there were a few patches of mildew on one middle-aged leaf only; in October there was a fair amount of mildew ( $S^2$ ) on the hops.

Ref. no. Z 4. 1918: Very mouldy ( $S^2$ ) on the leaves. 1919: No observations made. 1920: On August 28 there was one spot of mildew on one leaf; no observations were made in October.

Cuttings of W 56, Y 28 and Z 4 taken in the winters of 1918–19–20 all proved persistently immune in the greenhouse.

In 1919 eleven cuttings of OR 38 in pots were stood<sup>1</sup> in the hop-garden on June 13. On October 23 when all were examined one cutting<sup>2</sup> was found to be infected very slightly, there being a tiny “powdery” patch on the undersurface of two leaves. In this season fourteen clone-plants of OR 38 [which were of the same age as the cutting (noted above) which became infected and which had been potted up in similar soil] had been tested in the greenhouse and had all remained persistently immune. With regard to the plants in pots in the open, no mildew was present on them at the end of September. By the date October 23 several light frosts had occurred; it appears, then, safe to infer that the immunity of OR 38 was broken down or partly broken down by certain climatic conditions, possibly low temperature. (The case of Z 25, noted above, also supports this view.)

Ref. no. OR 39. This seedling on being raised in the greenhouse from seed in 1914 proved, like OR 38, to be persistently immune. In the hop-garden it showed, in 1916, a trace of mildew, two lateral shoots from the main stem having one leaf each bearing a few mildew-patches. In 1917 one small mildew-patch occurred on the undersurface of one leaf of a lately-developed sideshoot. In 1918, 1919 and 1920 the plant remained free from mildew, although its neighbour OR 38 was infected

<sup>1</sup> The pots were stood on a board, to prevent any contact between the plant, or the soil in the pot, and the soil of the hop garden.

<sup>2</sup> This was a cutting of the clone-plant W 56.

to the extent of  $S^3$ ,  $S^1$  and  $S^2$  in those years respectively. In the greenhouse, 35 cuttings of OR 39 have all proved persistently immune when tested in various seasons.

Ref. no. OY 18. No mildew was present in 1918; a trace of mildew occurred in 1919 and 1920. The behaviour of its neighbours on either side was as follows: OY 17 (♀), 1918,  $S^2$ ; 1919,  $S^1$ ; OY 19 (♀), 1918 and 1919,  $S^3$ .

Ref. no. DD 31. A trace of mildew occurred in 1919, which was the first season after the seedling had been planted out in the open. As a young non-flowering plant it remained persistently immune in the greenhouse for three consecutive seasons (1916–17–18). In 1920 no suitable material for infection was present in the hop-garden in the autumn.

Ref. no. HH 20. This seedling showed a trace of mildew in 1918. Its neighbour HH 19 (♀) was  $S^3$  in 1918, and its other neighbour HH 21 (♂) was  $S^2$ . No suitable material was available in 1919, and the seedling was then grubbed up for want of room.

Ref. no. HH 44. A trace of mildew occurred on this seedling each season from 1917 to 1919; in 1920 no suitable material was available. Its neighbour HH 43 (♀) was  $S^2$  in 1918 and 1919.

Ref. no. II 13. In 1918 a minute patch of mildew occurred on one leaf only. No suitable material was available in 1919 and the plant was then grubbed up for want of room.

Ref. no. II 24. No mildew occurred on this seedling in 1918 and 1919; its two neighbours, II 23 (♀) and II 25 (♀) were both  $S^2$  in 1918.

Ref. no. II 30. In 1918 this seedling remained free from mildew, although a lateral shoot of II 31 (♂) which was virulently affected with mildew twined round it. No suitable material was available in 1919 and 1920.

Ref. no. 316. A minute trace of mildew occurred in 1919 and in 1920—in the latter season the small patches of mildew were confined to the undersurface of one leaf only.

Summarising the histories of the 27 seedlings which are immune in the greenhouse we find that 5 seedlings (Z 2, Z 17, Z 42, II 24, II 30) have remained immune in the hop-garden. All these are ♂ plants and as such have been less severely tested under the special conditions noted above (p. 149) than the ♀ seedlings; further, two of them (Z 17 and II 30) have obviously been insufficiently tested. Taking the evidence as a whole, one is led to the conclusion that in all probability these five seedlings need only some particular weather conditions, coupled with a certain stage of growth, to show in the open at least the  $S^1$  stage of susceptibility.

It is interesting to find that the majority of the seedlings fall into the class in which susceptibility in the open varies from O to S<sup>1</sup>. Of these seedlings six (V 92, V 93, Z 14, Z 31, OR 39, OY 18) are males, and five (V 91, Z 25, OA 49, OB 34, OD 19) are females. The injury caused by the mildew to plants which show a susceptibility of only S<sup>1</sup> grade would be negligible from the practical or commercial standpoint, so that these twelve seedlings could be classified as "commercially resistant<sup>1</sup>."

The six seedlings (OE 14, DD 31, HH 20, HH 44, II 13, 316) which so far have shown only S<sup>1</sup> in the open would similarly come into the "commercially resistant" class, if they can be considered sufficiently tested.

The two (female) seedlings (Z 20, Z 22) which have varied in susceptibility in different seasons from O to S<sup>2</sup>, and the one (female) seedling (OA 34) which has varied from S<sup>1</sup> to S<sup>2</sup> have so far suffered so little injury from attacks of the mildew that they also can be included in the class of "commercially resistant," notwithstanding the fact that the grade of susceptibility may reach to S<sup>2</sup>.

The (female) seedling OR 38 has varied in susceptibility from S<sup>1</sup> to S<sup>3</sup>, and in the season of 1918 (and to a less extent in 1917 and 1920) the crop of hops was appreciably damaged. It is perhaps significant that this is the seedling which showed one season a local and temporary susceptibility in the greenhouse (see above, p. 154).

While, therefore, as OR 38 clearly shows, the possession of immunity under greenhouse conditions is not infallibly an indication of immunity, or even of "commercial resistance," in the open, it does appear that at any rate a majority of the seedlings which show immunity in the greenhouse possess, when grown in a hop-garden under commercial conditions, a sufficiently high degree of resistance to be classified at "commercially resistant."

In all, 301 cuttings, taken from most of the 27 seedlings enumerated above, have been rigorously tested in the greenhouse from 1917 to 1920, and all have been found to be immune. In no case has any seedling of the wild hop which has proved immune in the greenhouse in any one season shown susceptibility when cuttings from it have been tested in the greenhouse in other seasons. Cuttings have been taken from "immune" seedlings (*e.g.* Z 2, Z 14, Z 25, Z 42, OB 34) after they have been growing for five years in a fairly heavily manured hop-garden, and from

<sup>1</sup> To remove any possible misconception, it may be stated here that none of these seedlings of the wild hop have any direct commercial value.

one seedling (OR 38) after it has shown a high degree of susceptibility ( $S^3$ ) in the hop-garden; in all cases the cuttings have shown the original persistent immunity. There is no indication so far that cultivation has had any effect whatever in changing or modifying the original inherent "constitutional" character of the seedling.

As will be seen from Table IV, tests have been made in various seasons with certain seedlings to prove the continuance of their susceptibility under greenhouse conditions. Not only seedlings which are mildewed to the degree  $S^3$  in the open, but also seedlings, like OA 25, which in certain seasons show only a trace of mildew in the hop-garden, proved fully susceptible in the greenhouse.

If we contrast the excessive susceptibility under greenhouse conditions of the cuttings of the seedlings Z 24, Z 26, Z 41 and OD 18 with the absolute immunity of the cuttings of Z 25, Z 42, OD 19—remembering that all the cuttings were taken at the same time from the parent-plants which had been growing for five years in the hop-garden within a few feet of each other—we have the most convincing evidence of the permanence of different "constitutional" characters in seedlings of the wild hop.

(b) *"Semi-immunity" under greenhouse conditions.*

On reference to Table III, it will be seen that 7 seedlings (Z 15, Z 23, Z 38, OC 6, BB 5, OA 33, OD 17) have shown "semi-immunity" in the greenhouse. The behaviour of these seedlings in the hop-garden has been as follows:

Ref. no. Z 15. 1917, 1918, 1919: A medium attack of mildew ( $S^2$ ) on the hops. In 1917 and 1918 its neighbour Z 16 was mildewed to the extent of  $S^3$ . In 1920 Z 15 showed on several of its youngest leaves the arrested or circumscribed development of the mildew-patches characteristic of "semi-immunity"; otherwise the plant was free from mildew.

Ref. no. Z 23. 1917: Mildewed to the extent of  $S^2$  on the hops. 1918: No mildew present. 1919: A trace of mildew. 1920: No suitable material present. The neighbouring seedling Z 24 was so susceptible that each season it became mildewed to the highest degree, and in 1918 and 1920 the crop was destroyed by mildew.

Ref. no. Z 38. 1917, 1918: Mildewed to the extent of  $S^2$  on the hops. 1919: No mildew present, although some of the lateral shoots of Z 38 twined round the stems of Z 39, which bore very mildewed hops. Z 39 has each season been attacked  $S^3$ , and in 1918 had its crop entirely destroyed by mildew.

Ref. no. OC 6. 1917, 1918: No mildew present, while OC 5 (♀) and OC 7 (♀) were both mildewed  $S^2$  and  $S^1$  in those years respectively. 1919: OC 6 showed a trace of mildew; while OC 5 showed no mildew, and OC 7 a trace of mildew. 1920: No mildew present on OC 6, but a few leaves showed signs of having repelled mildew attacks; OC 5 was mildewed  $S^2$  (OC 7 had been grubbed up).

Ref. no. BB 5. 1918: A mere trace of mildew, while BB 4 (♂) and BB 6 (♂) were both mildewed  $S^2$ . 1919: No mildew present on BB 5 (BB 4 and BB 5 had been grubbed up). 1920: A trace of mildew.

Ref. no. OA 33. 1917, 1918: No mildew present, while OA 32 (♀) was mildewed  $S^3$  in both seasons. 1919: Both OA 33 and OA 32 were mildewed  $S^2$ . 1920: A minute trace of mildew on OA 33 (OA 32 had been grubbed up).

Ref. no. OD 17. 1917, 1919: This seedling showed considerable resistance to mildew, producing a good crop of healthy cones, while its two neighbours OD 16 and OD 18, growing on either side and so close that lateral shoots intertwined, were so severely infected that practically every cone was diseased. 1918: A mere trace of mildew in the cones, while the crop of OD 16 and OD 18 was destroyed by mildew.

Summarising the histories of the above seedlings, we find that two seedlings, OC 6 (♂) and BB 5 (♀) have varied in susceptibility in the hop-

Table V.

*Analysis of 480 seedlings of the wild hop.*

| Degree of susceptibility                                | No. of seedlings | %     |
|---------------------------------------------------------|------------------|-------|
| $S^3$ (including $S^{3+}$ ) each year }<br>(11 ♂; 85 ♀) | 96               | 20.00 |
| $S^2$ to $S^3$ (sometimes $S^{3+}$ ) }<br>(35 ♂; 80 ♀)  | 115              | 23.96 |
| $S^2$ }<br>(54 ♂; 26 ♀)                                 | 80               | 16.67 |
| $S^1$ to $S^2$ }<br>(41 ♂; 48 ♀)                        | 89               | 18.54 |
| $S^1$ }<br>(19 ♂; 12 ♀)                                 | 31               | 6.46  |
| O— $S^1$ }<br>(9 ♂; 9 ♀)                                | 18               | 3.75  |
| O }<br>(all ♂)                                          | 6                | 1.25  |
| O— $S^3$ }<br>(9 ♂; 18 ♀)                               | 27               | 5.63  |
| O— $S^3$ }<br>(all ♀)                                   | 3                | .60   |
| $S^1$ to $S^3$ }<br>(5 ♂; 10 ♀)                         | 15               | 3.12  |
|                                                         | 480              | 100   |

garden from O to S<sup>1</sup>, and that one seedling OD 17 (♀) has shown the grade S<sup>1</sup> consistently. These three seedlings may apparently be classed as "commercially resistant" in the open.

All the other seedlings are liable in certain seasons to be mildewed to the extent of S<sup>2</sup>.

As already mentioned, 480 seedlings have been planted out in the Experimental Hop-garden. In October of each year the susceptibility of each seedling has been noted. For the greater number of these seedlings, the records have been kept for four years (1917 to 1920). An analysis of these records gives us the following classification on p. 159.

Of the 480 seedlings, 189 (or 39.38 per cent.) proved to be males, and 291 (or 60.62 per cent.) proved to be females.

A separate analysis of the records of the two sexes gives us the following classification:

Table VI.

*Analysis of 189 ♂ seedlings of the "wild hop."*

| Degree of susceptibility       | No. of seedlings | %     |
|--------------------------------|------------------|-------|
| S <sup>3</sup>                 | 11               | 5.82  |
| S <sup>2</sup> —S <sup>3</sup> | 35               | 18.52 |
| S <sup>2</sup>                 | 54               | 28.57 |
| S <sup>1</sup> —S <sup>3</sup> | 41               | 21.69 |
| S <sup>1</sup>                 | 19               | 10.05 |
| O—S <sup>1</sup>               | 9                | 4.76  |
| O                              | 6                | 3.17  |
| O—S <sup>2</sup>               | 9                | 4.76  |
| S <sup>1</sup> —S <sup>3</sup> | 5                | 2.65  |
|                                | 189              | 100   |

Table VII.

*Analysis of 291 ♀ seedlings of the "wild hop."*

| Degree of susceptibility                                    | No. of seedlings | %     |
|-------------------------------------------------------------|------------------|-------|
| S <sup>3</sup> (including S <sup>3</sup> †)                 | 85               | 29.21 |
| S <sup>2</sup> —S <sup>3</sup> (sometimes S <sup>3</sup> †) | 80               | 27.49 |
| S <sup>2</sup>                                              | 26               | 8.93  |
| S <sup>1</sup> to S <sup>2</sup>                            | 48               | 16.49 |
| S <sup>1</sup>                                              | 12               | 4.12  |
| O—S <sup>1</sup>                                            | 9                | 3.09  |
| O—S <sup>2</sup>                                            | 18               | 6.19  |
| O—S <sup>3</sup> *                                          | 3                | 1.03  |
| S <sup>1</sup> —S <sup>3</sup> *                            | 10               | 3.44  |
|                                                             | 291              | 100   |

\* See remarks below at p. 162.

The percentage figures in the two tables given above show a higher grade of susceptibility among the ♀ seedlings than among the ♂ seedlings. It would be unsafe, however, to consider this proved, owing to the circumstance (see above, p. 149) that the observations as to the incidence of the mildew were made at a time peculiarly favourable for attacks on the ♀ plant. The ♂ and the ♀ plants would need to be tested at a time when each provided the same amount of infectible material before any inference could safely be drawn as to their relative susceptibility. Of the 27 seedlings showing immunity in the greenhouse, 14 are ♀ and 13 are ♂.

Since excellent material to test the degree of susceptibility was always present each year in the case of the ♀ plant, it will be safer to use the figures in Table VII rather than in Table VI on which to base an estimate of the percentage of the seedlings in various grades of susceptibility.

In the highest grade of susceptibility in which the plant was *each season* mildewed to the extent of  $S^3$ , there are 85 seedlings. Of these, no less than 34 had their crop of hops entirely destroyed in one or more seasons<sup>1</sup>.

In the next class, the incidence of mildew varied from  $S^2$  to  $S^3$  in different seasons. This class comprises 80 seedlings. Of these, 21 seedlings had their crop of hops destroyed by mildew in some season<sup>2</sup>. If we add together 34 and 21, we get 55 as the number of seedlings which have had the entire crop of hops destroyed in some season or seasons. This number represents 18.90 per cent. of the total number of the ♀ seedlings.

Referring back to Table VII, we may consider the first class of 85 seedlings showing  $S^3$  each season (which represents 29.21 per cent. of the ♀ seedlings) as exhibiting excessive susceptibility to mildew, probably greater than that shown by any commercial variety of hop cultivated to-day.

To the class of very susceptible seedlings may safely be added the 80 seedlings of the  $S^2$  to  $S^3$  class. This gives us 165 seedlings (or 56.70 per cent. of the total number) belonging to a grade of susceptibility in which virulent attacks of mildew are common.

<sup>1</sup> The actual records for these 34 seedlings are as follows, where the integer gives the number of seedlings, and the numerator of the fraction the number of times the entire crop was destroyed and the denominator the number of seasons during which observations were made:  $2\frac{3}{4}$ ,  $5\frac{1}{4}$ ,  $7\frac{1}{4}$ ,  $2\frac{3}{8}$ ,  $7\frac{1}{8}$ ,  $11\frac{1}{2}$ .

<sup>2</sup> In all cases  $S^{2+}$  was reached only once by these seedlings, the actual records being as follows:  $1\frac{1}{2}$ ,  $9\frac{1}{2}$ ,  $6\frac{1}{2}$ ,  $5\frac{1}{2}$ .

In the class  $S^2$ , consisting of seedlings which have shown a medium attack of mildew each season, we have 26 plants, or 8.93 per cent.

In the next class, where the incidence of mildew varies in different seasons from  $S^1$  to  $S^2$ —that is, from a trace of mildew to an attack of medium intensity—we have 48 plants, or 16.49 per cent. In this class an appreciable degree of resistance to the mildew begins to be shown by some of the seedlings, but it is in the succeeding classes that this phenomenon is most clearly seen. One seedling, however, in the present class proved to be commercially resistant.

In the class  $S^1$ , *i.e.* those seedlings which have shown only a trace of mildew each season, we have 12 plants. Of these, 5 cannot be considered to have been sufficiently tested, leaving us with 7 seedlings which have proved to be persistently resistant in the open. Among these 7 seedlings, there are 4 which are immune, and 1 semi-immune, under greenhouse conditions.

In the class  $O-S^1$  we have 9 seedlings, of which 1 has been insufficiently tested. These 8 seedlings are “commercially resistant” in the open; 5 of them are immune, and 1 semi-immune, under greenhouse conditions.

In the class  $O-S^2$ , in which there are 18 seedlings, 2 plants (both of which show immunity in the greenhouse) have proved to be “commercially resistant” in the open. The other seedlings in this class, while certainly showing resistance to the mildew, are liable to fairly serious attacks in some seasons, and therefore cannot be considered as “commercially resistant.” Among these are 2 seedlings which are immune, and 1 which is semi-immune, under greenhouse conditions.

The 13 seedlings in the classes  $O$  to  $S^3$  and  $S^1$  to  $S^3$  do not constitute in either case a proper group. Of the 3 seedlings showing  $O$  to  $S^3$ , one only possesses probably a slight degree of resistance. Of the 10 seedlings showing  $S^1$  to  $S^3$  in different seasons, 9 almost certainly belong to the  $S^2$  or  $S^3$  class, while the remaining plant is  $OR\ 38$  (immune in the greenhouse), which is fully discussed above (p. 154).

As constituting the group, then, of “commercially resistant” plants, we have the following 18 seedlings (representing 6.19 per cent. of the 291 ♀ seedlings), distributed in the following classes:

$S^1$  to  $S^2$ :  $OA\ 34$ .

$O$  to  $S^2$ :  $Z\ 20, Z\ 22$ .

$S^1$ :  $OC\ 25, OD\ 17, OE\ 14, FF\ 9, HH\ 20, HH\ 44, II\ 13$ .

$O$  to  $S^1$ :  $V\ 91, Z\ 25, OA\ 49, OB\ 34, OD\ 19, OY\ 24, BB\ 5, HH\ 9$ .

## SUMMARY.

1. The "wild hop" (*Humulus Lupulus* L.) is composed of a number of forms<sup>1</sup> which show distinctive physiological, or "constitutional," characters, as measured by the grade of susceptibility to the attack of the mildew *Sphaerotheca Humuli*. These characters vary from extreme susceptibility, shown both in the open and under greenhouse conditions, to a high degree of resistance in the open and complete immunity in the greenhouse. Of 291 ♀ seedlings, 165 seedlings, or 56.70 per cent., show extreme susceptibility, while 18 seedlings, or 6.19 per cent., are "commercially resistant" in the open. The remaining seedlings fall into groups representing intermediate grades of susceptibility.

2. Of 480 seedlings, ♂ and ♀, 27 seedlings, or 5.63 per cent., are completely immune—and 7 seedlings, or 1.46 per cent., semi-immune—under greenhouse conditions.

3. The majority of the seedlings which show complete immunity under greenhouse conditions show a high degree of resistance in the open.

4. The distinctive degree of susceptibility possessed by a seedling, both as shown in the open and under greenhouse conditions, has shown no change after the plant has been cultivated for five years in a manured hop-garden.

<sup>1</sup> The question as to whether these forms possess distinctive morphological characters is reserved for another occasion.

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## ON THE FLEECES OF CERTAIN PRIMITIVE SPECIES OF SHEEP<sup>1</sup>

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(With Plates I and II.)

### INTRODUCTION.

At the present time extensive breeding experiments between Black-faced ewes and Southdown rams are in progress with the ultimate object of improving the fleece of the Scottish hill-sheep. To this end precise knowledge of hair and of wool is necessary.

In the fleece of the Southdown there is but one kind of fibre, recognised as wool, while in that of the Blackfaced there are fibres very distinct one from the other and recognised as hair and wool respectively, and also other fibres appearing to be of intermediate character, the exact nature of which is not known. These indefinite fibres render the above experiment extremely complicated yet full of interest to the student of genetics.

They may possibly be the common ancestral type of fibre from which both hair and wool have sprung, or they may be but degenerate forms of hair or wool or of both.

An investigation of the characters, functions, and natural variability of the fleece of the wild and primitive species of sheep, some of which are known to have played a part in the production of the modern domesticated breeds, may throw considerable light upon this problem of wool-improvement and will provide standards to which the component fibres of the modern fleeces may be referred.

One of the distinguishing characters of mammals is the presence of hair. Classed according to the nature of its growth, it is of two kinds: temporary, being shed usually once a year and replaced by new hair, and permanent, having a perennial growth. The summer coat is not shed, it develops further to become the winter hair. The winter hair is shed in the spring, the new summer coat replacing it.

<sup>1</sup> A grant in aid of publication has been received for this communication.

But classed according to the length and structure of the hair there are two types also. One is relatively short and curled and is hidden by the longer, coarser, straighter kind. These two types of hair, because of the difference in their length and disposition, form two coats: an inner one of fine, curly fibres, forming an open-meshed mat snugly applied to the surface of the skin, and an outer one of stout, up-standing fibres, projecting well beyond the inner coat.

The two coats appear to serve different functions and this is associated with very distinct differences in structure. The outer one shields its wearer from excessive heat and cold, from wet, and from injurious contact with objects generally. It is cold- and heat-excluding, the general direction of its component fibres is such that it forms an efficient downward watershed, draining off the rain as it falls: its fibres present a surface upon which snow does not readily find a lodgment; and it protects the curly, delicate, fine hair of the inner coat from entanglement in thorny thickets.

The inner coat is heat-retaining in function, for in its meshes air is held. The inner coat is the wool of commerce. Many other mammals also possess this coat and it is a matter of conjecture why man chose the sheep as the source of his supply.

I am indebted to Professor J. Cossar Ewart, F.R.S., of the University of Edinburgh for the samples with which this study was made, and to Major H. J. W. Bliss of the British Research Association for the Woollen and Worsted Industries for much helpful criticism. A grant from the Carnegie Trust has enabled me to illustrate this paper with appropriate plates.

#### THE FLEECE OF *OVIS AMMON POLI*.

Marco Polo's "exceeding great wild sheep, having horns, some of them six spans long," are found on the mountain ranges of the Pamirs—"the roof of the world." They have been shot 18,000 feet above sea-level. The climate of this region is very rigorous, with long winters, rain and snow and bitter winds, but the water-courses and valleys are rich in mountain grasses, and even on the high passes in March snow is rarely so deep as to prevent the herds of the Kirghiz from finding pasturage.

Two samples from the summer and winter coats respectively were available for examination, and both were taken from the mid-dorsal line between the shoulders.

The summer coat (Pl. I, Fig. 1, left) on inspection showed one kind of fibre having the general appearance of hair as opposed to wool. But classed according to length and colour, there were three groups:

1. Numerous fibres uniformly 3 cms. in length and having shafts of uniform calibre. The free end of each was broken and each bore along its length the marks of numerous transverse fractures. In colour they were white in the proximal third and more or less pigmented a ruddy brown in their distal two-thirds.

2. Others, less numerous, were shorter, ending in unbroken, long, tapering tips and uniformly pigmented.

3. Complete, deeply and entirely pigmented, very small fibres, ranging from 1-7 mms. in length, forming a bristly mat upon the surface of the skin.

The winter coat (Pl. I, Fig. 1, right) was of two kinds, an outer one of hair similar to the longest hairs of the summer coat, and an inner coat of fine curled wool.

The great majority of the hairs were 5 cms. in length, some very slightly coloured and others entirely devoid of pigment. Not one possessed its tip and many had been broken off nearer the skin. No smaller or intermediate hairs were present.

The wool fibres when stretched to their fullest extent averaged 3.5 cms. in length, but there was considerable variation. The inner coat of wool formed a mat among the bases of the hairs 2 cms. thick.

The following measurements were made by Professor Barker of Leeds University for Professor Ewart.

| Sample                   | Hair  |        |                   |             |       | Wool   |        |                   |
|--------------------------|-------|--------|-------------------|-------------|-------|--------|--------|-------------------|
|                          | Diam. | Length | Waves<br>per inch | Diameter of |       | Diam.  | Length | Waves<br>per inch |
|                          |       |        |                   | Tip         | Root  |        |        |                   |
| <i>Ovis ammon poli</i>   |       |        |                   |             |       |        |        |                   |
| Summer coat              | ·009  | 1.1    | 3                 | ·002        | ·01   | —      | —      | —                 |
| Winter coat              | ·0103 | 1.6    | 5                 | ·005        | —     | ·001   | ·8     | 8                 |
| <i>O. ammon hodgsoni</i> | ·0107 | 1.0    | 6                 | ·00125      | ·0107 | ·001   | 1.03   | 20                |
| <i>O. ammon ammon</i>    | ·006  | 1.28   | 8                 | ·00105      | ·0071 | ·00075 | ·93    | 20                |

This table shows that there is no wool in the summer coat of Marco Polo's sheep. In the case of the other species only the winter coat was available for examination.

*The Hair* (Pl. I, Figs. 2a, 3, Pl. II, Figs. 4, 5). A transverse section of a typical hair from either the summer or the winter coat showed the following structure. A central medulla consisted of shrunken cells and cell-elements lying amid irregular spaces. Surrounding the medulla was the cortex, composed of several concentric layers of flattened cells. External to the cortex, the hyaline colourless scales of the cuticle were sought but though scores of hairs were carefully examined, after different methods of preparation

and with different methods of illumination, these scales, with their free edges typically directed towards the tip of the hair, could not be found until the heavily pigmented very small hairs from the summer coat were examined.

In the longer and older hairs the cuticle had disappeared (Pl. II, Fig. 4), probably by attrition during life, leaving the cortical cells exposed, and only near the bases of such hairs could remnants of the cuticle be found. In the case of the shorter and younger hairs the cuticle had been preserved since these hairs had been amply protected by the longer ones (Pl. II, Fig. 5).

The hair fibres were never entangled, and naturally do not felt as they are too straight, too stout, and too up-standing, and in the case of the young hairs upon which the cuticle is still present, the cuticular scales have free edges which are not serrated.

Figs. 2 and 3 show that the disposition of the pigment granules of a hair is such that they outline the cells of the cortex. It was found that when a winter white hair was mounted in weak balsam it assumed the coloration of a pigmented summer hair. This was possibly due to the withdrawal of air as the following experiment shows. A white hair, mounted in weak balsam and examined under the microscope, was subjected to gentle pressure along its length by means of a pencil-point. The hair ruptured, and air-bubbles rushed out, leaving the fibre pigmented. On removing the pressure the air rushed back and the hair became once more white.

The medulla of a hair could not be seen through the cortex, but it seemed that the spaces of the medulla were occupied by air which made its way among the cortical cells. If air comes to lie between the pigment of the cortex and the eye of an observer, the refractive properties of the air-film render the pigment invisible. The presence of air within a hair is associated with age: a white hair is an old hair. The air-film, moreover, gives a heat-retaining property to the outer coat and incidentally provides a protective coloration. It was found that the air-film prevented aqueous dyes from entering the fibres. It is suggested that kemp is such a fibre, a hair prematurely old.

*The Wool.* The wool fibre has the same essential histological structure as a hair save that it is finer—0.1 of the diameter of a hair—non-pigmented, and has many more waves to the inch. It is so constructed that it is impossible to distinguish between cuticles and cortex. One cell with free edges serrated and projecting towards the tip, occupies

the whole circumference of the fibre in striking contrast to the surface structure of a hair (Pl. II, Fig. 6 *a, b, c*).

In the majority of wool-fibres no medulla could be identified containing air-spaces, but in a few definite air-filled central areas were seen (Pl. II, Fig. 6 *d*).

#### THE FLEECES OF OTHER SPECIES OF SHEEP.

For purpose of comparison the hair and wool of *O. ammon hodgsoni*, *O. ammon ammon*, *O. vignei*, *O. montana*, and *O. orientalis* were examined. Save for certain minor unimportant differences, all were identical in structure and did not differ from the hair and wool of *O. ammon poli*.

In the case of *O. orientalis*, however, the character of the inner coat was remarkable in that instead of the fibres forming a much entangled mat (Pl. II, Fig. 7 *b*) as in the case of the other fleeces, they formed natural locks very similar in form to those of the wool of the modern breeds (Pl. II, Fig. 7 *a*). I am indebted to Professor Ewart for calling my attention to this interesting and perhaps important fact. Of all the primitive wools this most resembles in disposition the wool of commerce of to-day.

The two kinds of fibres in the fleeces of the primitive species of sheep were absolutely distinct and no sort or grade of intermediate fibre was found. Careful search for a fibre of intermediate character was made but without success, each fibre was either hair or wool, definitely and unmistakably. Thus the fibres of intermediate character found in certain modern fleeces cannot be regarded as transitional forms and the question as to whether hair and wool are different in their origin and development, or whether they result from the divergent development of a common type of fibre of intermediate character cannot be answered. The exact relation of hair and wool must be sought in other mammals.

The hair and wool of the primitive species of sheep may be accepted as the typical examples of these fibres and as standards to which the fibres in the modern fleeces may be referred.

#### SUMMARY.

1. The fleeces of certain wild and primitive species of sheep were examined.
2. That of Marco Polo's sheep was found to be the one most suitable for examination, since samples of both summer and winter coats were available. In the former coat there was hair only and still growing. In the latter coat it was mostly full-grown and much less pigmented. The

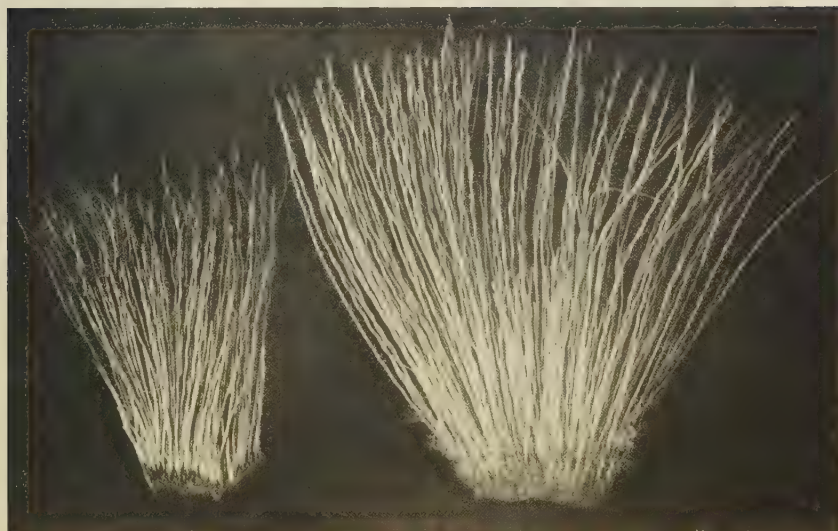


Fig. 1.



Fig. 2 *a.*



*b.*



*c.*

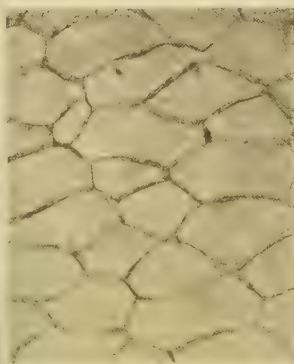


Fig. 3.





Fig. 4.



Fig. 5.

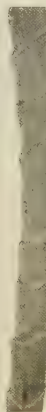
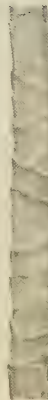


Fig. 6 *a*.



*b*.



*c*.



*d*.

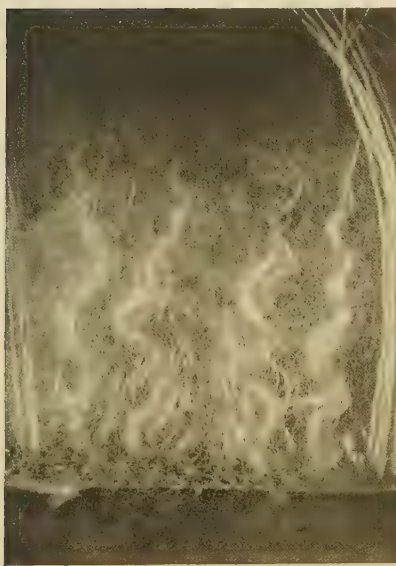
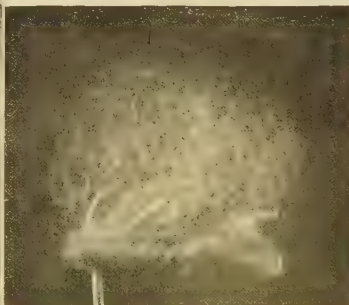


Fig. 7 *a*.



*b*.



white appearance was due to the presence of a film of air between the pigment granules of the cortex and the eye of the observer.

3. Wool is present in the winter coat but absent from the summer one.

4. The microscopical structure of hair and of wool are briefly described and attention is called to the disposition of the wool in the fleece of *O. orientalis*, since this most closely resembles that of the wool of the modern domesticated breeds.

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#### EXPLANATION OF PLATES I AND II

- Fig. 1. *O. ammon poli*. Summer (left) and winter (right) fleeces.  $\times 1\frac{1}{2}$ . In the summer coat the distal two-thirds of the longest hairs are pigmented; young heavily pigmented hairs form a dark mat upon the skin; there is no wool. In the winter coat the hair is longer and the tips are broken; there is much less pigment; there are no young hairs; and there is an inner coat of wool.
- Fig. 2. The cortical cells of hair.  $\times 110$ . (a) The hair of *O. ammon poli*; (b) of *O. ammon hodgsoni*; (c) of *O. ammon ammon*. The pigment is arranged around the cells.
- Fig. 3. The cortical cells of the mature hair of *O. ammon poli*.  $\times 450$ . The cells are those of the cortex; there is no overlapping and the cells are arranged in the form of a mosaic.
- Fig. 4. The lateral edge of a full-grown hair,  $\times 420$ , to show that there is no cuticle.
- Fig. 5. A young hair from the summer coat,  $\times 1230$ , to show the presence of the cuticular scales.
- Fig. 6. Wool.  $\times 600$ . (a) *O. ammon poli*. (b) *O. ammon ammon*. (c) *O. ammon hodgsoni*. (d) A fibre showing the presence of air-spaces within the medulla.
- Fig. 7. Wool.  $\times 3$ . To show the disposition of the fibres. (a) *O. orientalis*. (b) *O. ammon poli*.

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## OBSERVATIONS ON THE INSECTS OF GRASSES AND THEIR RELATION TO CULTIVATED CROPS

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### I. INTRODUCTION.

THE insects of grasses may be divided into two distinct groups, those which actually feed on the grasses and those which shelter among grass during the winter period. For the purpose of this paper particular emphasis will be laid on such insects as, while using grasses for shelter or food, finally migrate to cultivated crops for the completion of their life-history, for the development of later broods, or, as in the case of sheltering insects, for food when the crop is at the critical stage which satisfies their requirements.

That insect pests of cereals use grasses as intermediate hosts is a well-established fact (see Theobald<sup>(18)</sup>, Miall<sup>(11)</sup>, Washburn<sup>(19)</sup> and Lugger<sup>(10)</sup>). So far, however, little attempt has been made to establish definitely the part played by grasses in harbouring the pests, and we know very little of the degree of infestation of those which grow about our hedgerows and waste places. Accurate knowledge under this head would be of value to the agriculturist in controlling insect pests by the more efficient upkeep of hedges and ditches.

This subject for investigation was suggested by Dr A. D. Imms, M.A., to whom I am grateful. My thanks must also be expressed to Mr A. Roebuck, Head of the Department of Agricultural Biology at Harper Adams College, for information, suggestions and constant advice. The observations were taken over the period from mid-October 1919 until the end of June 1920.

The winter period was very mild and undoubtedly favoured the persistence of growth of plants and the continued feeding of many insects. The spring and early summer, however, was wet and cold with short periods of bright warm days, which state was so unfavourable that it was not until May 18th that the Frit Fly adults were observed on the oat crop.

## II. METHODS.

In order to arrive at some definite conclusion as to what insects are found feeding and wintering in grasses, examples of the various species dug up from headlands, hedgerows, waste ground and arable fields, were taken into the laboratory and examined, each shoot being cut open for careful scrutiny. The date, locality, species of host plant, and the number and variety of insect stages present were recorded for further consideration. Of the insects found some were preserved in spirit, others kept in captivity, if larvae or pupae, for examination in subsequent stages, while many were dissected for microscopic examination.

While the laboratory work was proceeding the crops growing on the College Farm were kept under observation and, where they were attacked by any insects of the species found feeding amongst grasses, data as to cultivations, date of sowing and infestation were secured. In this connexion particulars are included of the attack by Frit Fly on winter wheat in the early part of 1920.

Special note was taken of insects found sheltering in the plants examined, since definite information concerning the means whereby many insects pass the winter is lacking.

With regard to root-feeders such as "wireworms" and "Leather-jackets" the difficulty of taking them actually feeding presented itself, but where symptoms of attack in grasses and corn crops were identical it was considered justifiable to draw conclusions.

The foregoing may be considered as the winter methods, those obtaining in the summer period varying in that less time was spent in the dissection of grasses and more in observing the attacks of leaf-feeding and leaf-mining insects under field conditions. Here again arose the difficulty of the root-feeders and night-feeders, so that evidence of the larvae having eaten and their proximity to the attacked plant when taken were noted and inferences drawn.

## III. SOIL AND LOCALITY.

Most of the observations were made on the College Farm, where there are two main types of soil, viz. the heavier loams merging into clays and the lighter loams emerging into soils of sandy texture. Geologically these types are represented by the Lower Red and Mottled Sandstone and the Pebble Beds, both of the New Red Sandstone formation. The locality is approximately 220 feet above sea level and is exceptionally free from smoke of factory, foundry or town.

The rainfall is normally about 24·5 inches annually, falling chiefly in winter and spring.

The locality is well sheltered on all sides by belts and clumps of trees, chiefly elm, lime, ash and oak, and these, with the woods of the neighbourhood attract birds which, in their foraging doubtless destroy numbers of insects harmful alike to grass and arable land.

On the newly broken up grassland it was noticeable that pigeons, rooks, jackdaws, plovers and starlings spent most of their time, in preference to the older arable fields the insect life of which had attained its normal level.

Grasses grow very luxuriantly here so that there is abundance for such insects as infest them, hence the effect of insect migration is felt continuously.

#### IV. HARVEST TO SPRING SOWING—WINTER PERIOD.

##### Table of Insects Feeding and Host Plants.

|                                     |   |                                                                                                                                         |
|-------------------------------------|---|-----------------------------------------------------------------------------------------------------------------------------------------|
| 1. <i>Coleoptera</i> :              |   | Host                                                                                                                                    |
| <i>Agriotes obscurus</i> , L.       | . | <i>Arrhenatherum avenaceum</i><br><i>Dactylis glomerata</i><br><i>Lolium italicum</i>                                                   |
| <i>Athous haemorrhoidalis</i> , F.  | . | <i>Cynosurus cristatus</i><br><i>Lolium perenne</i>                                                                                     |
| <i>Melolontha vulgaris</i>          | . | <i>Agrostis stolonifera</i><br><i>Poa pratensis</i><br><i>P. trivialis</i>                                                              |
| 2 <i>Hymenoptera</i> :              |   |                                                                                                                                         |
| (Unidentified)                      | . | Galls on <i>Agropyrum repens</i>                                                                                                        |
| 3. <i>Lepidoptera</i> :             |   |                                                                                                                                         |
| <i>Apamea secalis</i> , Bjerk.      | . | <i>Dactylis glomerata</i><br><i>Agrostis stolonifera</i><br><i>Lolium perenne</i><br><i>Poa pratensis</i><br><i>Trisetum flavescens</i> |
| <i>Triphaena pronuba</i> , L.       | . | <i>T. flavescens</i><br><i>Poa pratensis</i><br><i>Lolium perenne</i>                                                                   |
| <i>Agrotis exclamationis</i> , L.   | . | <i>L. perenne</i><br><i>L. italicum</i>                                                                                                 |
| 4 <i>Diptera</i> :                  |   |                                                                                                                                         |
| <i>Cecidomyia destructor</i> , Say. | . | <i>Agropyrum repens</i><br><i>Dactylis glomerata</i>                                                                                    |
| <i>Cecidomyia</i> spp.              | . | <i>Agropyrum repens</i><br><i>Dactylis glomerata</i><br><i>Lolium perenne</i>                                                           |

|                                         |                         |
|-----------------------------------------|-------------------------|
| Oscinis frit, Linn. . . . .             | Trisetum flavescens     |
|                                         | Arrhenatherum avenaceum |
|                                         | Agrostis stolonifera    |
|                                         | Holcus lanatus          |
|                                         | Lolium perenne          |
| Pachyrrhina imperialis, Mg. . . . .     | L. perenne              |
|                                         | L. italicum             |
|                                         | Arrhenatherum avenaceum |
|                                         | Holcus lanatus          |
|                                         | Bromus sterilis         |
| Tipula oleracea, L.                     | Lolium italicum         |
|                                         | Arrhenatherum avenaceum |
|                                         | Agrostis stolonifera    |
|                                         | Poa pratensis           |
| Sciara spp. . . . .                     | Trisetum flavescens     |
| 5. <i>Thysanoptera</i> :                |                         |
| Limothrips cerealum, Hal. . . . .       | Dactylis glomerata      |
|                                         | Holcus lanatus          |
|                                         | Lolium perenne          |
| 6. <i>Hemiptera</i> :                   |                         |
| Macrosiphum granarium (Kirb.) . . . . . | Arrhenatherum avenaceum |
| 7. <i>Collembola</i> :                  |                         |
| Sminthurus luteus (Lubbock) . . . . .   | Lolium perenne          |
| Orchesella cincta (Linn.) . . . . .     | L. perenne              |

Of the insects feeding in winter, we find among the Coleoptera the larvae of the click beetles. "Wireworms" as defined by Roberts(14) are "The larvae of the genus *Agriotes* and that of *Athous haemorrhoidalis*." Their distribution is somewhat localised for Ford(7) says that in Cheshire he found the common wireworm as the larva of *Agriotes obscurus*. A similar state of affairs obtains in Shropshire where *Agriotes obscurus* predominates, *Athous haemorrhoidalis* coming second in order of importance. In this district the wireworms were found in greatest numbers on sandy soils having abundance of humic matter in the form of root fibres. Land recently broken up was badly infested and calculations showed in several fields numbers varying from 26,780 to 331,700 wireworms per acre, the former case existing after a crop of linseed. The larvae of *Athous haemorrhoidalis* apparently prefer pastures and meadows to arable land; only two specimens were taken in arable land and then on land which had been broken up in 1918. They were fairly numerous along hedgesides where they attained great size, feeding amongst the roots of grasses and hedge plants. Some difference of opinion still prevails as to the mean depth of wireworms in the soil. During the winter careful examination of nine fields, seven of which were arable, showed that the majority of larvae were located from 1 inch to 4 inches below

the surface, except in the case of an attack of spring oats in April and May when they were found in the top inch of soil, many actually crawling out of the soil to attack the stems of young plants above the soil line. Numerous cases of larvae boring upwards in the stem were observed, the most persistent larvae being those of *Agriotes obscurus* from 8–12 mm. in length; in conjunction with this attack the various Tipulid larvae were also doing considerable damage.

The characters of *Agriotes* larvae as given by Roberts<sup>(14)</sup> enabled these wireworms to be readily distinguished. Roebuck in the 1918 Report of the Intelligence Department, Plant Disease Branch, states that "a downward movement of these larvae to protect themselves from cold was not apparent." This has been verified, the wireworms being taken within 3 inches of the surface on frosty mornings, and, even after continued frost, no migration to lower depths was observed.

The larvae of *Melolontha vulgaris* were found chiefly in meadows and waste land, feeding on any available decaying herbage. They showed a distinct preference for lighter soils and were consistently taken in heaps of road scrapings which had been left along roadsides. Here the larvae thrived, the compost of soil, grit, manure and decaying vegetation being evidently most favourable for them. No specific attack was noticed in the locality, though the larvae are reported as attacking mangels in Carnarvonshire in 1917 and potatoes in Norfolk, Surrey and Cardiff in 1918, those in Surrey being grown on an old lawn which had been broken up during the winter<sup>(1)</sup>.

*Lema melanopa* and *Sitones lineatus* were frequently found sheltering, the former head foremost in the hollowed portion of the stems of tall oat and cocksfoot grasses, and the latter low down amongst the dry dead leaves of cocksfoot, particularly in the vicinity of a field of "seeds." The attack of *Sitones* spp. on leguminous crops is very universal and on a field of beans 32 weevils were collected either feeding or resting from 62 plants, this was about 11 o'clock on a mid-April morning. Curtis<sup>(6)</sup> alluding to this ubiquitous weevil in 1844 states, "I well remember that in April and May I could not find a pea-field where the lower leaves of some plants were not eroded, the beans were equally marked."

The Hymenoptera are represented by only one species which formed galls on couch grass. This insect, which has not been identified, was found only during the winter and spring and I have found no instance of its being taken on any other grass or on any cereal crop.

The most predominant Lepidopteron was *Apamea secalis*. The larvae were found feeding internally in the base of the shoots of both grasses

and cereals from October till the beginning of June. The smaller, and therefore younger, larvae work upwards and the older ones downwards in the stem, the latter case being probably after migration from one plant to another, or from one shoot to another, and just prior to pupation. In only one case was a larva found externally and that on a stem of Golden Oat grass, possibly it was migrating or seeking a site for pupation—it eventually died after two days in captivity.

In February, *Apamea* larvae were found in conjunction with frit larvae attacking winter wheat ("Iron" variety) taken after seeds.

In 1918 similar attacks are recorded on wheat and oats in Shropshire, Hampshire and Wiltshire—being especially noted on ploughed up pasture. One is inclined to the belief that the larvae of *Apamea secalis* feed indiscriminately on grasses or cereals in almost any situation, be it pasture, meadow, headland, hedgerow, waste land, roadside, or grasses on bare patches in arable fields. An examination on May 31st of self-sown wheat and oats growing amongst clover and beans showed that of 28 tillers of wheat four were attacked, while in oats only one out of 24 suffered from *Apamea*.

The larvae of the *Agrotis* spp., specimens of which were taken feeding on the roots of perennial rye grass, were reported as attacking the young plants of wheat and oats in Staffordshire and Shropshire in 1918.

*Triphaena* larvae were taken feeding on the roots of golden oat grass; they are, however, general in their feeding habits and often go to rye grasses and meadow grasses.

The larvae of *Odonestis potatoria* which feeds on various grasses was taken on cocksfoot but was not observed to attack any cereal crop. One *Tortrix* spp. was taken feeding on oats and on the tall oat grass: it was small, about 8–10 mm. varying in colour from sooty to grey, sparsely hairy and exceedingly active. It fed both internally and externally. So far, attempts at rearing it have proved unsuccessful.

Among the Diptera, the Hessian Fly was found exclusively on Cocksfoot, as many as five pupae being taken from a single node. A specimen was also found on couch grass. Examination of cocksfoot grasses in autumn and early winter showed large numbers of empty pupal cases from which the autumn brood had hatched, also many pupae, which were kept and from which adults emerged in May. Records of attack by this fly are as follows: (1917) "Attacks by this fly on wheat were recorded from Durham, Lancashire (where it was abundant on a crop of late sown wheat near Birkenhead), Shropshire and Oxfordshire (fields of 'Sensation' wheat destroyed)"..."and in the Eastern Counties."

In 1918 a "slight attack in combination with *Oscinis frit*" is recorded<sup>(1)</sup> at Ormskirk, while at Harper Adams Agricultural College there was an attack on "Square Heads Success" wheat. Theobald mentions the second brood as attacking couch and timothy grasses, so far, however, I have not taken it on timothy. Allied to the foregoing are species of *Cecidomyia* which were found in great numbers on decaying vegetation during the winter. The "red maggots" accompanied "frit" and "Apamea" in their attacks on wheat and grasses. Larvae were taken on couch, cocksfoot, golden oat and perennial rye grass—the "red maggots" so characteristic are perhaps more saprophytic than parasitic in habit, especially is this so with cocksfoot grass.

The Frit Fly, *Oscinis frit*, was found first on November 19th when twelve larvae were taken from one plant of *Arrhenatherum avenaceum*—the tall oat grass. The plant was growing in the hedgerow bordering a field in which oats were badly attacked previously, so evidently the autumn brood had been egg-laying in the neighbouring grasses. Later, larvae were found feeding in perennial rye grass, golden oat, *Holcus lanatus* and *Agrostis Stolonifera*. In early February an attack, previously mentioned, on wheat after "seeds" was noted in a field on the College Farm and on examination the following infestation was calculated: Plants "Fritted," 27 per cent; plants attacked by *Apamea* spp., 1.05 per cent. In several cases two "frit" larvae were found feeding in the same stem. Regarding burying "frit" and their migration, eight "frit" larvae *in situ* in wheat plants were buried at a depth of 4 inches in a 9-inch pot of medium loam and above were planted four healthy wheat plants and four oat seedlings with the second leaves showing. Though the pot was kept under constant observation none of the plants were attacked but grew vigorously and healthily and no perfect insects were observed to emerge. Collin<sup>(5)</sup>, however, notes emergences from larvae buried from 7 inches to 9 inches deep.

Of root-feeders there were noted *Pachyrrhina imperialis* Mg., *Tipula oleracea* and the larvae of a Sciarid. The first-named feeds on plants in general, in the more moist parts of the field, preferring the rank growth near hedges, though it was found feeding amongst the roots of italian rye grass growing amongst beans. The larvae of *Tipula oleracea*, the common "Leather Jackets," were very destructive to barley seedlings in spring on newly broken-up grass fields of a moist character the soil of which was sandy and humic overlying clay. They are universal feeders and Roebuck<sup>(1)</sup> calculated in three different grass-fields 220,000, 13,000 and 120,000 larvae per acre.

Cameron(2) records the larvae of a species of Sciarid occurring "in small masses at the roots of grasses on which they were in all likelihood feeding."

Of the Hemiptera one species alone was observed, viz. *Macrosiphum granarium*. In 1917 "This aphid was reported as very abundant and causing considerable damage in the Eastern Counties, Oxfordshire, Shropshire and Staffordshire on wheat and oats in July and August(1)." This insect was found on tall oat grass, singly in early autumn, and again in the summer period. Attacks on oats were simultaneous with attacks on hedgerow grasses.

*Limothrips cerealium* (Hal.) was the only Thysanopteron taken. It feeds through the winter, in the larval stage in hollow-stemmed grasses. In 1917 "A distinct case of considerable damage to "Giant Eliza" oats at Newmarket (Cambs.)" was recorded(1)—though Thrip attack is fairly general but often overlooked.

Two species only of the Apterygota were noted—*Sminthurus luteus* and *Orchesella cincta*. These developed in great numbers on a plant of perennial rye grass obtained from a damp waste place and kept indoors. No definite attack was noticed. Cameron states, with reference to the Apterygota as a whole, "As a rule they do not penetrate very deeply into the soil generally being found in the first three inches. In many cases where members of this order have been reported as doing damage to root crops, I doubt very much whether they are the direct agents of injury. The chances are that they are merely what we term 'followers of decay' accentuating the evil that has been caused by other pests." In 1914 Roebuck, referring to damage to wheat and the presence of *Isotoma palustris*, writes(16): "These sheltered in tiny holes in the ground and were never caught on the wheat, and, therefore, may have caused none of the damage." Subsequently, however, he tells me they were abundant on wheat but were never seen actually feeding.

#### V. SPRING SOWING TO HARVEST—SUMMER PERIOD.

In addition to practically all those mentioned under "Winter Period" the following insects were observed feeding or sheltering in grasses.

##### *Coleoptera:*

|                                 |                                |
|---------------------------------|--------------------------------|
| <i>Rhizotrogus solstitialis</i> | Grass roots in meadows         |
|                                 | <i>Dactylis glomerata</i>      |
|                                 | <i>Lolium italicum</i>         |
| <i>Lema melanopa</i> , L.       | <i>Agropyrum repens</i>        |
|                                 | <i>Arrhenatherum avenaceum</i> |
| <i>Sitones lineatus</i>         | Amongst grasses in hedges      |

*Hymenoptera:*

|                                 |                                  |
|---------------------------------|----------------------------------|
| <i>Pachynematus clitellus</i> } | { <i>Poa trivialis</i>           |
| <i>Dolerus haematodes</i> }     | { <i>Arrhenatherum avenaceum</i> |

*Lepidoptera:*

|                              |                           |
|------------------------------|---------------------------|
| <i>Odonestis potatoria</i> . | <i>Dactylis glomerata</i> |
| <i>Hepialus humuli</i> .     | <i>Lolium italicum</i>    |
| <i>Arctia caia</i> . .       | <i>Dactylis glomerata</i> |

*Diptera:*

|                               |                         |
|-------------------------------|-------------------------|
| <i>Agromyza nigripes</i> .    | <i>Agropyrum repens</i> |
| <i>Rhyphnus fenestralis</i> . | <i>Lolium talicum</i>   |

During the summer period attacks on both grasses and Cereals were noticed by wireworms, leather jackets, surface larvae, weevils and apions. Since most of these insects have been dealt with under the previous section only those not mentioned there will here receive consideration.

*Rhizotrogus solstitialis* is a general feeder in the larval stage and like other chafer grubs does damage on broken-up grasslands and to the crops taken after clovers, following up the ravages of Cockchafers. The first "slugworm-like" larvae of *Lema melanopa* were observed in June 16th feeding on oats. In the same field last year large numbers were noticed attacking the wheat. In 1917 "*Lema melanopa* L. was noticed as very abundant on wheat in Kent and Shropshire in July. This insect is often mentioned in connection with cereal crops abroad but in this country seldom attracts attention (1)."

Regarding the two Sawflies, *Pachynematus* and *Dolerus*—in June 1919 ten larvae were taken feeding on the leaves of wheat—they were placed on a wheat plant growing in a 9-inch pot and covered with muslin — and finally the greater number pupated. They remained undisturbed in the soil until the early summer, 1920, when from May 10th to 13th four emergences occurred. The first to emerge died but the next two were put on an oat plant under a bell-jar and soon ovipositing was in progress. The larvae from these eggs hatched, but owing to a mischance escaped and were lost. Shortly after (June 13th) a similar larva (8 mm. in length) was taken on the tall oat grass and on July 5th a fully-fed one measuring 18 mm. was found on a similar clump of tall oat. The sites where the larvae were found both in 1919 and 1920 are identical.

Among the Diptera, *Agromyza nigripes*<sup>1</sup> was first observed on June 17th when eight larvae were found mining the leaves of three wheat plants. In 1919 they were observed feeding exclusively on wheat plants, but in 1920 they seemed to have extended their sphere of activity and numbers were found on oats and couch grass. Larvae taken in June

<sup>1</sup> Very kindly identified by Mr J. E. Collin.

1919 pupated after about three days in the top  $\frac{1}{4}$  inch of soil and emerged in May 1920; this would indicate that there is but one brood per annum. Field observations, however, showed some almost fully-fed larvae in June and some very small ones feeding about a month later—possibly there are two broods in a period of about eight weeks.

A single larva of *Rhyphus fenestralis* was taken with some larvae of *Pachyrrhina imperialis* feeding around the roots of italian rye grass in June. Cameron records it in decaying vegetable matter and one specimen at the root of *Senecio Jacobea*.

Of the Lepidoptera, *Odonestis potatoria* and *Arctia Caia* were taken feeding on grasses; the former is a general grass feeder, mostly taken on cocksfoot, the latter is a frequenter of waste places feeding, *inter alia*, upon *Lamium* spp. and cocksfoot. I have taken the latter in one instance feeding on seedling crucifers in frames though it is not generally observed as attacking farm crops.

Hepialis larvae are very common on waste places and amongst grass, they feed on any roots, and according to Theobald they are "found during winter in hop-stacks and devouring the roots of grasses, where they are extremely difficult to destroy." I have taken them at the roots of rye grass and clover in April. The soil was medium loam containing abundance of root fibres.

The Tortrix larva as mentioned under "Winter Period" was again observed on italian rye grass and in several instances feeding on oat leaves. It was invariably taken singly and probably does little damage.

## VI. NATURAL ENEMIES.

In the course of my work I have reared two parasitic Hymenopterons, one from *Agromyza nigripes* and one from *Cecidomyia destructor*; so far, however, I have been unable to identify them. Most soil larvae are subject to the attacks of various insect parasites and Roberts notes instances of Proctotrupids emerging from larvae of *Athous haemorrhoidalis* and mentions parasites of *Agriotes obscurus* being observed probably "also referable to the family Proctotrupidae." I have kept a close watch on wireworms in captivity but have obtained no parasites.

Carnivorous ground beetles such as *Steropus madidus* and *Nebria brevicollis* are said to be enemies of wireworms and in both adult and larval stages attack many soil larvae. In one instance I added to a pot of soil eight wireworms and one larval *Steropus* spp. and subsequent examination showed but four wireworms all within the bottom 2 inches of soil. As escape was impossible it is safe to conclude the missing wire-

worms were destroyed either by the Carabid larva or by the remaining wireworms.

Examination of a lark's nest containing fledglings showed the following insects dead or badly damaged:

- 4 adult *Tipula oleracea*.
- 2 larvae of *Tipula* spp.
- 1 „ *Apamea* spp.
- 3 "Surface larvae."

Jackdaws probably do much good in destroying insects, slugs, etc. One family consisting of, probably, two adults and three young birds visited a "seeds" field, after the crop had been cut, persistently for about a week at the end of June, evidently searching for slugs, beetles and insects in general. Hooper<sup>(8)</sup> gives an instance of a jackdaw being shot, when taking food to his brooding mate, the beak contents on examination revealing thirteen wireworms, four grubs and a few other insects.

#### VII. SUMMARY.

1. Insects which are parasitic alike on grasses, cereals, and other crops will, when these latter are unavailable, take up their quarters in the grasses and plants growing in the situations herein mentioned and, when the crops are again available return to them and commit their ravages.

2. Observations were conducted over a period of nine months on certain insects which attacked both grasses and cultivated crops in a limited area in Shropshire, viz. the farm of the Harper Adams Agricultural College, near Newport, and the immediate neighbourhood.

3. The observations indicate a danger of harbouring pests among the vegetation on headlands, hedgerows and waste places; grasses in particular, being susceptible to their visitation, are decidedly important factors in tiding pests over from season to season and this in itself suggests the advisability of keeping hedgerows and headlands clean.

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# STUDIES ON THE APPLE CANKER FUNGUS, I. LEAF SCAR INFECTION<sup>1</sup>

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(With 2 Text-figures and Plate III.)

FOR some years an investigation of the biology of the apple tree canker fungus has been proceeding at Long Ashton(1), and the work has now reached a point when the results can be published in detail. This paper will be confined to the infection of the leaf scars by the fungus. The ultimate object of the investigation was to find some means of control of this disease, and as a preliminary step it was necessary to find out how the fungal parasite entered the living tree.

Only incidental references are made to the literature of the subject as a summary of the work already published is given by Cayley(2).

The apple canker fungus is usually spoken of as a "wound parasite," and it is commonly supposed that, provided no agency is allowed to wound the host, infection is impossible. In the case of the canker fungus this view needs modification, since this fungus enters the normal healthy tree without any previous external injury. In fact, a most important path of infection is through the scars left by the fallen leaves. *Nectria ditissima*<sup>2</sup> therefore is only a wound parasite, if we include in the term "wound" such natural ruptures of external tissues as those occurring in the normal growth of the plant.

## INCIDENCE OF LEAF SCAR INFECTION.

The infection of canker through leaf scars is responsible for a large percentage of the canker at Long Ashton. This type of infection occurs on many varieties and is regular in its incidence, whilst from material received from South Devon, Worcester and Somerset, it would also appear to be widely distributed. In cider orchards (which under normal

<sup>1</sup> A grant in aid of publication has been received for this communication.

<sup>2</sup> No opinion is expressed regarding the name of *Nectria galligena*, Bres. recently suggested for the canker fungus.

conditions are not pruned) some of the varieties canker very badly and in these cases leaf scar infection is almost wholly responsible.

The association of canker with buds has been pointed out by Goethe (3).

Excellent material for studying this method of infection was afforded by some trees raised in the course of fruit-breeding work at Long Ashton. They were seedlings of the cross Kingston Black  $\times$  Médaille d'Or, two cider varieties, and developed canker very freely. In August 1919 numerous examples of young cankers evidently started from buds formed in the preceding autumn were found and these left no doubt that the canker fungus could enter the tree by some means in the region of the buds. Continuous observations have since been made on these trees.

The first point noticed was that the cankers on the 1918 wood were considerably in excess of those formed in the previous years. Counts of the cankers on the wood formed in five consecutive years gave the following results: on the 1915 wood, 1 canker; on the 1916, 4; on the 1917, 29; and on the 1918, 434. The number of 1919 was over 600, but exact figures were not obtained. On these trees, infection of the shoots took place during the year succeeding their formation, viz. the 1915 wood was infected in 1916, the 1916 in 1917 and so on. The trees in question had never been pruned and therefore the number of cankers formed on the growth of any one year gave an indication of the number of infections occurring during the following season.

The number of infections in some cases was exceedingly high. Taking a single branch of one of the trees, not more than  $1\frac{1}{2}$  ins. in diameter at its base and about four to five years old, almost every bud of the 1918 wood on that branch was cankered, the numbers reaching the very large total of 65. Besides the actual cankers, there were cases where the buds of 1918 failed to develop in the spring of 1919 and were possibly killed off by the fungus or at least so injured as to be unable to develop whilst the main stem remained uninfected. Such shoots, during August, showed long stretches of bare stem, and a tree severely attacked presented a partially defoliated appearance.

Large numbers of bud infections having been observed on the trees above mentioned, search was made to find similar infections on other varieties. Leaf scar infection was found to be extremely common, in fact so widespread as to give the impression that it would affect any variety provided the conditions were favourable. It has been found on Warner's King, Bramley's Seedling, James Grieve, King of the Pippins, Lord Suffield, Devonshire Quarrenden, White Transparent, Royal Jubilee and many other dessert and culinary varieties and also on many

cider varieties such as Kingston Black, Cap of Liberty and Strawberry Norman. There is, however, marked difference in the susceptibility of varieties. A striking instance of this was afforded in one of the plantations at Long Ashton where varieties growing adjacent to each other have behaved in characteristic manner during the last two winters. A record of the number of new infections occurring on the different varieties in the winter 1919–20 was as follows: Cox's Orange Pippin, no bud infection; King of the Pippins, 49; Worcester Pearmain, 1; Devonshire Quarrenden, 149; Beauty of Bath, nil. A particularly interesting point about this result is that Cox's Orange Pippin is usually regarded as extremely susceptible to canker, whilst Worcester Pearmain is by no means a resistant type. In view of the normal susceptibility of the King of the Pippins it is interesting to note that in another plantation a little distance away a row of this variety showed no canker at all. Anyone drawing conclusions from the behaviour of the trees on the above-mentioned plot would be completely misled as to the susceptibility of the varieties concerned. The explanation of this behaviour is at present obscure, but there are obviously many factors, such as, for instance, the vigour of the tree, the influence of the rootstock, the condition of the soil, or some inherent quality of the sap, about which we know very little at present and which may supply the key to the mystery.

The period of infection in the case of the Kingston Black  $\times$  Médaille d'Or seedlings is limited almost completely to the spring. The first infection of the 1919 wood of these seedlings was found on March 31, 1920, but after this date infection proceeded rapidly. During the winter 1920–21 three infections of the 1920 wood were found as early as February 1921. On most varieties, however, a large percentage of the infection takes place in the early autumn immediately after defoliation. During the last autumn (1920) infection of the lowest leaf scars of that year's growth occurred in many cases before the upper leaves had fallen. The rapidity with which infection took place was very striking, in some cases practically every shoot being attacked before defoliation was half completed. Generally speaking, therefore, there are two periods when leaf scar infection is especially active—(a) in the early autumn, and (b) in the spring. It is not suggested, however, that infection entirely ceases at other times of the year, in fact it appears to continue throughout the summer and with certain varieties during the winter, but the spring and autumn are periods when infection is markedly prevalent.

Comparing the severity of the attack of the winter 1919–20 with that of 1920–21, it would appear that the latter season was specially

favourable to the fungus. For instance, the first examples of leaf scar infection of the 1919 growth were not found until January 3, 1920, when three cases only were discovered in a plantation of 230 trees of 22 different varieties. In 1920-21 the intensity of infection varied very much, but some of the trees were very severely attacked as early as September 23. It is probable that weather conditions influence the incidence of canker as well as other diseases and one of the conditions most favourable to its spread seems to be rain, which was excessive during the early autumn of 1920. On the other hand, during the previous summer, the trees suffered from a severe attack of aphid and this undoubtedly weakened the trees and possibly rendered them unable to resist infection.

Whilst, as already pointed out, infection may take place on partially defoliated shoots in the autumn, at the scars of the recently fallen leaves, yet no scar infection has been observed so long as the leaf remained attached to the shoot at that point. The most vigorous trees of each variety retained their leaves longer than the weaker ones and were usually more resistant to canker. Cox's Orange Pippin, Worcester Pearmain and Beauty of Bath each retained their leaves till the end of October. The Médaille d'Or > Kingston Black seedlings referred to above also held their leaves till very late. Some attempt was made to correlate the periods of defoliation with susceptibility to canker and although, generally speaking, those varieties which are very susceptible defoliate early and those which are resistant are on the whole late, the differences between the two do not appear to be sufficiently marked to warrant any significant conclusion.

An interesting point worthy of notice is that the varieties which are susceptible to canker frequently show a similar susceptibility to *Fusicladium dentriticum*. This correlation is independent of the infection of scab wounds by *Nectria*, an account of which will possibly be published later. One sometimes finds shoots which are scabbed down one side of the stem only and in the shoots of King of the Pippins and Devonshire Quarrenden, the scabbed sides also bear numerous leaf scar infections. The conditions governing scab infection must evidently be similar to those governing leaf scar infection of canker. The side of the stem attacked by the scab and canker fungi is usually that exposed to the prevailing winds, which at Long Ashton come from the south-west. It may be that the lowering of the temperature of the exposed side of the stem retards the formation of the protective phellogen just sufficiently long to allow the fungus to infect.

In addition to infection of the recently formed leaf scars, occasional infections of a stem two or three years old take place in the region of a dormant bud. Such infections are readily distinguishable, at least in their early stages, by their similarity in appearance to the infections on the young wood, by the lack of any swelling of the stem and the absence of concentrically arranged fissures which are so characteristic of cankers of long standing.

#### STAGES IN THE DEVELOPMENT OF LEAF SCAR INFECTION.

In order to find out how the infection is brought about, search was made for the early stages of bud infection.

The seat of infection appears to be associated with the base of the bud rather than the interior of the bud itself. The earliest stages of infection are sometimes not visible externally at all and the bud has a normal appearance. It is only on cutting the stem that the infected tissues can be discovered and in many cases it is found that a small lateral portion of the leaf scar is infected, although the colour of the bark and the appearance of the bud are perfectly normal.

The first visible external signs of any disorder varies in different cases, but is usually associated with a small crack in the leaf scar. The sap of the apple stem quickly oxidises to a bright reddish brown colour on exposure to air and this property of the sap enables small injuries to the leaf scar tissue to be detected fairly readily. On strongly grown shoots, such as the "leaders" springing from the crown of the trees, no visible split develops at all, the first stage of infection being seen in the formation of a circular dark reddish brown spot on the main stem at the extreme edge of the leaf scar. This spot, at first the size of a pin's head, increases rapidly to about the size of a pea.

The next definite stage in infection is the development of the primary scar, *i.e.* the scar first limited by the newly formed phellogen. This development arises rapidly and varies in position according to the exact spot where infection first took place; it is usual, however, to find it rather below the leaf scar and more often in a lateral position than a median one (Plate III, Fig. 1). When once the fungus has entered the stem, growth is extremely rapid and it is only a short time before the stem is completely encircled. The tissues of the bud being young and succulent are very quickly attacked by the fungus, so quickly indeed that it is often difficult to obtain a young leaf scar infection in which the bud itself is not infected with mycelium. The separation of the cuticularised layers of the bark from the underlying cortex frequently occurs, and these form a

ragged membrane over the scar. Pustules of conidia are sometimes found on the primary scars in January and February and these show the extraordinary vigour with which the fungus flourishes during the dormant period of the host. Plate III, Fig. 2 shows young infections on the Médaille d'Or  $\times$  Kingston Black seedlings, which only become infected in the late spring and the cankers therefore develop slowly. Typical leaf scar infections as they appear in summer are shown in Plate III, Fig. 3.

The development of the canker after bud infection may be so rapid that the whole of the shoot above it is killed almost immediately. On the other hand, development may be slow and the canker may take three or more years before it completely encircles the stem. It is possible to find many cases of cankers on old wood which can well be attributed to leaf scar infection (Plate III, Fig. 4).

#### MICROSCOPIC DETAILS.

Observation of the development of the canker showed that in many cases at least, the infection started from the leaf scar and not from the bud itself. The leaf scars were therefore examined minutely. The dead tissues of the leaf scar were invariably found to be infested by fungi, one interesting fungus not yet identified being almost universally present. It has been found on the leaf scars within a week of defoliation and very rapidly gains a foot-hold on the scar tissue. It has dark coloured mycelium and is associated with a pycnidium containing dark, olive green, muriform pycnosporos (Text-fig. 2). The pycnidia are sometimes immersed in the leaf scar tissue or they may occur outside seated on a small mass of hyphae. In addition to the pycnidia, dark coloured conidiophores are commonly found bearing spores similar to *Fumago vagans*, but whether these fructifications belong to the same fungus as produces pycnidia is unknown. The fungus has been noted upon specimens from Cambridge and Worcestershire and is probably of common occurrence. Whether this fungus plays any part in bringing about infection is not known, but such a possibility cannot be overlooked and therefore its occurrence is recorded here.

In the infection of leaf scars in the early autumn, no case of infection was discovered whilst the leaf remained attached to the tree, although numerous instances were found but shortly after defoliation. Inoculation experiments through the scars of freshly removed leaves during June 1919 were completely unsuccessful, although two inoculations of wounds with the same inoculant produced typical cankers. At the normal fall of the leaf in the autumn, however, the host is not in as active state of

growth as in June. When a leaf falls, the tissue exposed is submitted to the desiccating effects of the atmosphere and results in the drying up of the cells exposed. The contraction of the tissue which takes place on drying results in small cracks appearing in the leaf scars, especially in the region of the soft tissue adjacent to the leaf traces. These small cracks allow the canker fungus the opportunity to enter the host, which it does very readily, before the host has had time to form a phellogen (Text-fig. 1). The small depressions between the leaf scars and the main stem hold up small quantities of water which probably aid the germination of the spores of the fungus. The tissue of the leaf base is rather looser than the normal cortex and the canker fungus grows very freely in the intercellular



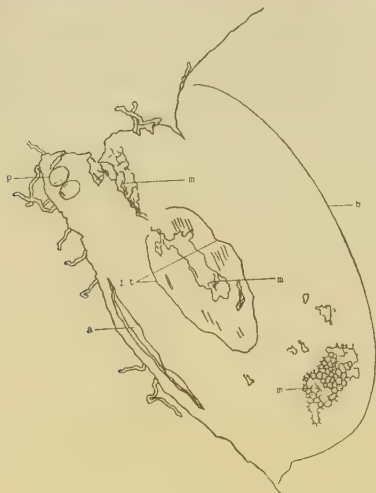
Text-fig. 1. Radial longitudinal section of a leaf base showing a crack in the leaf scar and the mycelium about to enter the host. The intercellular space in the tissue below the crack affords an unimpeded entrance to the fungus.  $\times 34$ . *m* = mycelium; *l.t.* = leaf trace; *i.s.* = intercellular space.

spaces. The spread of the fungus is helped by the slow response of the host to form a limiting phellogen, and the stem soon becomes completely girdled (Text-fig. 2).

The second period of infection, which takes place when the trees become active in the spring, however, is very similar in its symptoms to the autumn infection. Many tiny cracks in the leaf scar tissue are found especially towards March and April when the buds are bursting. Throughout the winter the buds gradually swell by normal growth, but the swelling is usually sufficiently slow to allow the continuity of the phellogen to be maintained. The growth cracks, however, frequently extend to considerable depths. With the enormous increase in growth in early

spring, fissures arise which expose the tissues of the leaf base and readily allow the canker fungus to enter. The host only slowly reacts against the fungus which therefore quickly develops, in many cases surrounding the stem and killing off the shoot above it.

The view that the cracks resulting from the growth of the buds, afford a means of entrance to the fungus in the spring, is also strengthened by the observation, given above with regard to the times of appearance of bud infection. The Médaille d'Or  $\times$  Kingston Black seedlings are



Text-fig. 2. Radial longitudinal section showing infection of the leaf base and the crack through which the fungus first entered. There is no sign of phellogen formation and the mycelium has penetrated deeply in the intercellular spaces. An infection of *Venturia inaequalis* can be seen on the outside of the stem.  $\times 25$ . *m* = mycelium; *l.t.* = leaf trace; *b* = limit of infected region; *p* = pycnidia; *a* = *Venturia inaequalis*.

naturally exceptionally late in bursting into leaf, but until this takes place only very occasional infections can be found on the previous season's growth. It appears that there is a definite correlation between the appearance of canker and the swelling of the buds on the Kingston Black  $\times$  Médaille d'Or seedlings and this fact points to the conclusion that the growth cracks which accompany bud development allow the entrance of the fungus.

A point of interest which may be mentioned here is that further infections of the canker fungus on the Kingston Black  $\times$  Médaille d'Or

seedlings do not always develop into cankers, owing to the formation of a phellogen which excludes infected material in exactly the same way as has been found to exist when shallow cuts are inoculated artificially. Such excluded material can be recognised hanging on to the edge of the infected leaf scar (Plate III, Fig. 2).

#### CONTROL CONSIDERATIONS.

The economic loss by the leaf scar infection is considerably reduced in the case of bush trees by the practice of winter pruning. In this process, most of the infected wood is cut out, although some is occasionally overlooked, and also infection may take place after the pruning has been done. In the case of young trees the loss is especially important, as a large quantity of new growth is required to build up the main stems. A few bud infections on a young tree usually means a considerable loss to the tree. At Long Ashton not a few cases of grafts of varieties so resistant as that of Bramley's Seedling, have been totally destroyed by infection of the leaf scar. With orchard trees, where little pruning is done, this type of infection is most serious, and it is probable that in those cases where the trees suddenly canker all over, it is leaf scar infection which is responsible for the damage. The sudden increase in the number of infections on the Kingston Black  $\times$  Médaille d'Or seedlings, as recorded above, shows that such a state of things does occur.

There does not appear to be any valid reason why spraying of the leaf scars, especially before the buds burst, should not prove a successful control measure in the case of spring infections of the canker fungus. Preliminary trials<sup>(4)</sup> with this end in view were started in December 1919. Twenty branches were selected from the Kingston Black  $\times$  Médaille d'Or seedlings and ten of these branches were sprayed with copper stearate on December 16, 1919, the remaining ten being left as controls. Counts made on May 23, 1920, showed that the number of new cankers on the sprayed branches was reduced from 299 in 1919 to 62 in 1920, whilst the number on the controls increased from 135 in 1919 to 299 in 1920. Additional infections took place subsequently, but in December 1920 re-counts showed a marked reduction on the sprayed branches, the numbers then being 179 for the sprayed and 500 for the controls. These results are sufficiently promising to warrant the further trials which are now being carried out.

Reference must be made here to the spraying experiments carried out by Grubb<sup>(5)</sup> at East Malling during the last two years. By spraying with lime-sulphur or Bordeaux, in May and again in June, he was able

to record a considerable reduction of canker infections. The best times for spraying are obviously immediately after defoliation or before the breaking of the buds and it is somewhat difficult to see why spraying in May and June should be markedly effective. Until defoliation in the autumn no infection would occur on the 1920 wood and it is doubtful if spraying in May or June would affect this appreciably. As regards the 1919 wood, however, the main autumn and spring infections would also have occurred before the sprayings and would not be affected by them. But as already mentioned the leaf scar infection of the previous season's wood continues slowly throughout the summer and possibly against this infection the spraying was effective.

The existence of autumn infection of leaf scars naturally increases very considerably the difficulty of the control of the disease by spraying in the case of varieties so affected. First of all the spraying of the leaf scars immediately after defoliation is dangerous, because at that time the fruit still remains hanging on the tree in many instances and spray fluids may spot the fruit. Further, the spraying of ripe fruit with a copper fungicide is open to obvious objection, and as regards sulphur sprays as an alternative, the fact that the canker fungus does not appear to be very sensitive to sulphur rather discounts their effectiveness<sup>(6)</sup>. Another difficulty in autumn spraying for canker is the rapidity of infection, which results in many leaf scars being infected before defoliation is complete. At least two sprayings at the time of defoliation therefore would appear to be necessary to control the disease even if suitable spray fluids can be found.

Although spraying treatment for autumn infection therefore is not altogether promising, other treatments for reducing the amount of infection may yet be possible. Vigorous trees usually hold their leaves longer than weakly ones and any treatment therefore which would tend to increase the vigour of the trees, may by delaying autumn defoliation reduce the risk of infection.

#### SUMMARY.

The infection of the apple stem by the canker fungus through the leaf scars is described.

The fungus appears to enter through small cracks which appear in the leaf scar tissues, in the autumn immediately after defoliation and in the spring when the buds are swelling.

The possibility of preventing this infection by disinfecting the leaf scars by fungicides is discussed and results of preliminary trials recorded.

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## EXPLANATION OF PLATE III.

- Fig. 1. Early stage in the infection of a shoot of Devonshire Quarrenden. The fungus entered at the edge of the leaf scar and the boundary of the infected tissue can be distinguished. March 1920.  $\times 1$ .
- Fig. 2. Infections on Kingston Black  $\times$  Médaille d'Or seedlings. The infections are about three months old. At A, a portion of infected tissue can be seen isolated and excluded from the stem. August 1920.  $\times \frac{2}{3}$ .
- Fig. 3. Typical leaf scar infections on Tom Putt, Middle Winter Pippin and an unknown variety of apple. Note that each scar surrounds a bud. August 1920.  $\times \frac{2}{3}$ .
- Fig. 4. Cankers on the 1917 and 1918 wood of Bramley's Seedling, probably developed from leaf scar infections. August 1920.  $\times \frac{1}{2}$ .

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Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.



ON THE LIFE HISTORY OF "WIREWORMS" OF  
THE GENUS *AGRIOTES*, ESCH., WITH SOME NOTES  
ON THAT OF *ATHOUS HAEMORRHOIDALIS*, F.<sup>1</sup>

PART II.

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(With 4 Text-figures and Plate IV.)

EXTERNAL STRUCTURE OF *AGRIOTES OBSCURUS*, L.

THE first part of this paper contained an account of the biology and life-history of *Agriotes*. This part contains descriptions of *Agriotes obscurus*, L. in the oval, early and late larval stages, together with observations on the pupa. The stages are taken in their natural order, but since an acquaintance with the later stages for the sake of brevity has been presumed in describing the early ones, it may perhaps be necessary to refer to the general description of the final instar in some cases. In addition, it has been considered desirable to describe the mouth parts and spiracles of the larva in greater detail than was possible in a general description. Separate sections for each of these have therefore been added.

In the third part of the paper it is hoped to give some description of the larva of *Agriotes sputator*, L. with some notes on the early stages of *A. sobrinus*, Kies. = *acuminatus*, Steph. and *Athous haemorrhoidalis*, F.

I must again express my gratitude to Dr Russell and the Committee of the Lawes Agricultural Trust for the facilities given me at Rothamsted for carrying on the earlier stages of this part of the investigation, as well as for the figures reproduced in the plate. The later stages have been completed at Cambridge through the kindness of Prof. Stanley Gardiner, to whom my thanks are also due. I wish further to express my indebtedness to Mr C. Forster Cooper and Dr Hugh Scott for kindly allowing me during the last six months to work in the Cambridge Zoological Museum and to make use of the books and collections there.

<sup>1</sup> A grant in aid of publication has been received for this communication.

## THE EGG.

Generally broadly ovoid, but irregular in both shape and size. Average dimensions of four ova  $.59 \text{ mm.} \times .47 \text{ mm.}$  A fifth measured after fixation  $.64 \times .40$ . Shell transparent, exhibiting the milky-white yolk and embryo within. The germinal band of the embryo appears as a yellowish-green stripe. The surface of the shell is almost smooth, though a few irregular shallow punctures are visible under the microscope.

## FIRST LARVAL INSTAR.

The young larva on hatching is about 2.5 mm. in length and less than .4 mm. in breadth across the prothorax. It is milky white in colour, shining, but when examined under the microscope is found to be minutely punctured and wrinkled. It has the general appearance of being broader and more stumpy than the later stages. Only the mouth parts are yellow, the mandibles being darker still and quite brown at their apices. The 9th abdominal segment is pointed and somewhat constricted at about two-thirds of its length. All the setae are colourless, the eye spots black. The head and all the body segments, with the exception of the 9th and 10th abdominal segments are broadest in the middle and somewhat rounded at the sides. The cauda and margins of the sensory pits of the 9th abdominal segment are colourless, so that the latter are difficult to make out in life. The marginal striae at the base of the body segments, though present, are also only to be made out with difficulty.

Throughout the first instar the larva remains pale and semitransparent, though at the end its general colour has become faintly yellow. The margins of the sensory pits on the 9th abdominal segment are then visibly brown, the constriction near the end of the same segment has been lost and the anterior half of the segment has its sides subparallel, while the posterior tapers to a point at the cauda, which is still colourless or almost so. Five larvae taken from the pots at this age measured 3.25–3.5 mm. in length.

The following points may also be noted in which the young larva of the first instar differs in greater or less degree from the full-fed larva.

Sides of the head subparallel. It is broader than long, measuring the breadth across the middle and the length from the insertion of the mandibles to the base of the head.

Instead of the three-pronged nasale or clypeal process, the latter is represented by a single-toothed process, twice as broad as long and blunt at the apex (Fig. 2 e).

In the antenna the 3rd or supplementary segment is proportionally longer than the same segment in full-fed larvae, being two-thirds the length of the 1st and 2nd segments combined.

The mandibles are broader in proportion to their length than those of the full-fed larva, the width at the base being rather more than two-thirds of their length. The apex is finely pointed and considerably incurved. The eye spot is pitchy, situated somewhat further from the base of the antenna than in the full-fed larva and is more conspicuous.

The nervous ganglia, which are plainly visible through the integument in stained preparations, are in proportion to its size very large in the young larva. The two lobes of the supra-oesophageal ganglion, situated in the prothorax and extending backwards into the mesothorax are especially noticeable. There are thirteen ganglia in all, as is common in coleopterous larvae. The spiracle itself is rather more rounded in the young larva, the breadth across the two orifices being greater in proportion to the length than in older larvae. The teeth on either side of the stigmatic orifices are few in number, being about seven or eight in the thoracic and six in the abdominal spiracles.

At first the peritreme is almost colourless, but later it becomes yellow, though it is less strongly chitinised than in older larvae. Each orifice is bordered separately by its own peritreme, so that the two orifices have the appearance of separate spiracles with a small interval between them. At the anterior end of each the peritreme disappears and the boundary to the orifice is merely the unthickened cuticle.

The hairs situated on the tergites between the mesothoracic and 8th abdominal segments are pale, the posterior row slightly longer than the length of the segments to which they belong, the anterior short. In the prothorax, however, where the segment itself is longer than the other segments, the hairs in both rows are considerably shorter than the segments and are about equal to one another. On the 9th segment the hairs surrounding the apex are noticeably long and the posterior hairs of the head are also long, being longer than the anterior hairs and as long as those on any other part of the body.

#### SECOND INSTAR.

As already stated (Pt. I, p. 126) the first ecdysis takes place in June. The larva is then of about 3.5 mm. in length. In the second instar its growth is much more rapid and at the end it has attained a length of 5.5-6.5 mm. and breadth of about .5 mm. The colour of the larva is now pale yellow and the body is quite opaque. The tergites are nearly smooth,

but under the microscope can be seen to bear numerous short irregularly shaped striations. The sternites are smoother.

The segments of the body are cylindrical or pearly so, but the head is flattened dorso-ventrally and is somewhat darker in colour than the remaining segments.

The setae are slightly yellowish and all are shorter than the segments to which they belong. The setae of the posterior row are longer than those of the anterior, as in older larvae.

The marginal striae at the base of the 2nd and 3rd thoracic and of the abdominal segments are very fine, but are visible under the microscope. Similarly, those forming the anterior and posterior margins of the prothorax.

The nasale, or clypeal process, is now trifid, with a stout median dens and a smaller lateral dens on either side of the median one, scarcely half as long and little more than half as broad as the median one. Ventral to the nasale the semi-lunar process over the mouth, described in the older larva, can now be identified. In the specimen in which it was found four or more teeth could be seen, the remainder being represented by the sinuate margin of the process. The proportion of length to breadth of the mandible now nearly corresponds to that of the full-fed larva. In the antenna the dorsal process at the apex is still proportionately longer than in the late stages, being about one and a half times the length of the 2nd segment.

The spiracles are now distinctly margined by a brown peritreme, which however is pale and very narrow on the anterior margin of each respiratory orifice. The posterior margin is also narrow but more distinct. The lateral margin and also the central septum are broader than those of the first instar and furnished with pittings or corrugations corresponding to the number of teeth which project from the sides of each orifice. These number eight or nine in the abdominal and eleven in the thoracic spiracles.

The stigmatic scar is visible as a colourless strand in the chitin placed at an obtuse angle to the axis of the spiracle and dorsal to it. The inner end is attached to the atrium, while the outer terminates in a slightly divaricate fork in the cuticle.

The 9th abdominal segment is subparallel at the sides for nearly two-thirds of its length. It then tapers sharply to the apex, from which the cauda is produced. The latter is distinct, sharply pointed and in colour tinged with yellow.

The sensory pits are bordered by an ochraceous rim which is elevated

above the surrounding area chiefly at the sides. Behind, it is less raised and paler in colour.

### THIRD INSTAR.

The second ecdysis occurs at the end of July or in August and the larva passes its second winter in the third instar. At the beginning it is about 6-8 mm. in length and  $\frac{1}{2}$  mm. in breadth. In colour it is distinctly yellow and in other respects also except size closely resembles the full-fed larva.

The tergites are sparsely punctate but bear numerous irregular striations, which may be seen under a low magnification.

The sternites are smoother. Setae distinctly yellow. Nasale trifid, with median dens the stoutest. Dorsal process of antenna about equal to the second segment.

Spiracles are now distinctly different from those of *A. sputator* at the same age, being shorter and proportionally wider.

The teeth or corrugations at the sides of the orifices number eight to ten in the abdominal and fourteen in the thoracic segments.

The stigmatic scar is thicker than in the previous instar.

The 9th abdominal segment is broadest just posterior to the sensory pits and from that point gradually tapers to the distinctly pointed cauda. Sensory pits margined on all sides with brown.

The following table gives some idea of the actual increase in length of the larva during the early instars. All the larvae hatched in 1916 (or 1918) and were afterwards kept in pots under normal conditions as far as possible.

| Instar          | Date of observation | Average length mm. | No. of specimens | Range of length mm. |
|-----------------|---------------------|--------------------|------------------|---------------------|
| First (1st day) | Aug. 1916 (1918)    | 2.5                | 5                | 2.0 — 3.0           |
| „ (9 months)    | May 1917            | 3.35               | 5                | 3.25 — 3.5          |
| Second          | End July 1917       | 5.75               | 6                | 4.5 — 6.5           |
| Third           | Mid Sept. 1917      | 6.82               | 7                | 5.75 — 8.5          |
| Fourth          | End July 1918       | 9.25               | 2                | 8.5 — 10.0          |
| Fifth           | End Aug. 1918       | 10.46              | 14               | 8.25 — 13.0         |
| Eighth          | Early July 1920     | 17.0               | 3                | 16.0 — 18.5         |

If this table of records is compared with the estimate made in Part I of this paper (p. 127) it will be seen that the larvae were about a year behind the estimate in 1920. It seems likely, therefore, that the length of life in the larval stage is, or at least may be, of six years' duration<sup>1</sup>.

<sup>1</sup> Some confirmation of this forecast has been obtained since the above was written. Of three larvae of the 1916 brood, on August 22nd, 1921, one was found to have developed into an imago (♀), a second remained a larva (of length 22 mm.), the third was not found, possibly having attained maturity and so having been overlooked in the soil.

## GENERAL DESCRIPTION OF THE LARVA IN FINAL INSTAR.

Length 22-26 mm.; breadth 1.75-2.0 mm.

Apart from the head and 9th abdominal segment nearly cylindrical: yellow, usually rather pale.

*Head* quadrangular, slightly broader than long, flattened above and beneath: somewhat darker in colour than the remaining segments. Wider behind than in front, bearing a long seta near each of the four angles, besides several shorter ones situated chiefly anteriorly: punctures sparse and irregular.

Upper surface with an elongate-oval plate (the cephalic plate), which is expanded anteriorly over the base of each mandible. Anterior margin of the plate, over the entrance to the mouth, with a strongly chitinated brown process, which divides into three sharply pronged denticles, the middle one being the longest. Anterior angles of the head slightly rounded.

*Antennae* situated close to the base of the mandibles, short, consisting of two segments and two processes borne separately at the apex of the 2nd segment. Ventral process shorter, conical and nearly colourless; dorsal process darker and more strongly chitinated, linear and about equal in length to the preceding segment. Probably the latter should be regarded as the 3rd segment.

*Eye spot* dark brown or black, situated laterally, a little below the base of the antenna.

*Mandibles* rather small, stout, yellowish brown, with sharply pointed, pitchy black apices: each bearing two denticles on the inner margin and a brush-like process, the penicillus, at the base.

Ventral surface of the head with a pair of somewhat oblique furrows, brown, nearly straight and reaching from the base of the mandibles to points beyond the base of the hypostome, also with two ridges of darker brown chitin, somewhat bowed, situated in the cavity between the epicranial plates (genae) and the maxillae and nearly reaching the posterior apices of the cardines.

*Maxillae* (Fig. 1) each with a very short cardo, articulating with the tentorium at its second branch. Stipites somewhat rounded on their outer margins and straight within. Palps yellowish-brown, composed of four segments and borne on white membranous palpigers at the apices of the maxillae. Galeae composed of two segments, with a small thimble-shaped process at the apex. Laciniae small, triangular, sharply pointed and densely margined with wavy hairs on their inner margins. Terminal

lobe of the *labium* approximately pentagonal, wider in front than behind, bearing two long yellow setae. Labial palps two-jointed, the first segment with several setae near its apex. Between the bases of the palps, the margin of the labium is usually somewhat produced and probably represents the ligula. Mentum transverse, broader than the submentum, almost membranous. Submentum almost tongue-shaped, usually strongly

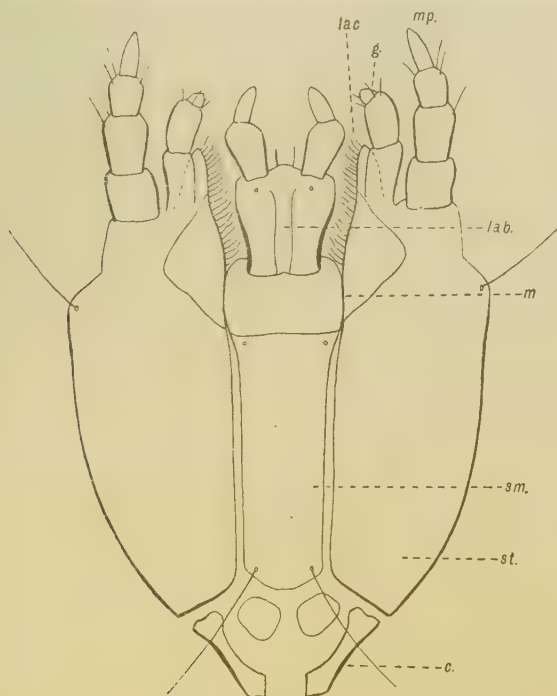


Fig. 1. Hypostome of larva (*R. Green del.*). *c*=cardo; *st.*=stipes; *sm.*=submentum; *m*=mentum; *lab.*=apical portion of labium; *mp.*=maxillary palp; *g.*=galea; *lac.*=lacina.

chitinised, with the anterior and lateral margins nearly straight, terminating in a blunt point posteriorly. A long seta is borne at each of the four lateral angles.

*Prothorax* nearly as long as the meso- and meta-thorax taken together. Both anterior and posterior margins of the pronotum have a border of fine longitudinal striations, the anterior extending somewhat further than

the posterior margin. The edge of the border is defined by a transverse brown line and a transverse series of minute pores, which are almost equidistant from each other. The meso- and meta-notum, as also abdominal segments 1-8, have the border only on the posterior margin.

The pronotum, like the tergite of each succeeding segment up to the 8th abdominal segment, is separated from the pleura by a narrow suture, running from one marginal border to the next. The pleura of the prothorax is, however, nearly triangular in shape instead of being parallel-sided as in the other segments.

Prothoracic *sternum* large, pentagonal, with its apex extending almost to the anterior coxae. Sterna of the meso- and meta-thorax narrow, nearly parallel-sided but somewhat broader in the middle. All *coxae* are surrounded by striations, concentrically arranged around their bases, except on the inside. They are rather long and pale and bear on their anterior and posterior faces a number of short, stiff, brown bristles. Each is approximate to its pair. A small brown spot, having the appearance of a pore, is placed near the lateral margin of the coxa.

Each succeeding segment of the leg is considerably shorter than the coxa and the broadest little more than half its breadth.

*Trochanter* much longer on the inner than the outer side, *femur* on the outer than the inner.

*Tibia* about equal in length to the femur but more slender. *Tarsus* consisting of a single segment, narrowed at a short distance from the base into a long, sharp, almost sickle-shaped claw.

The inner margins of the trochanter, femur and tibia bear short stiff bristles like those of the coxa, evidently of use in progressing through the soil. There are also two long fine setae attached to the inner margin of the trochanter, and one to the femur, as well as a whorl of rather shorter fine hairs round the base of the tarsus. The outer margin of the leg bears only a few fine, short hairs.

On the upper surface the *cuticle* is shallowly sculptured with fine punctures and irregular sutures, its general appearance being much smoother than in that of *A. sputator* (Plate IV, figs. *b* and *c*). The area anterior to the spiracles is smooth, or almost so. There is a fine medio-dorsal suture running from the anterior margin of the prothorax to the posterior margin of the 8th abdominal segment interrupted in its course only by the marginal striations already mentioned.

The tergite of each segment from prothorax to 8th abdominal segment bears two transverse rows of six rather long yellow hairs near the anterior and posterior margins respectively, the posterior hairs being

about twice the length of the anterior. The prothorax has a further row of short hairs rather variable in number close to the anterior marginal border. The ventral surface of the thorax is bare save for three pairs of short hairs on the prosternum. On the abdominal sternites 1-8 three rows are present bearing four, two, four hairs respectively.

The single pair of thoracic *spiracles* is situated in the pleurae of the mesothorax; those of the first eight abdominal segments near the lateral margin of the tergites a little behind the anterior margin (Plate IV, fig. *a*).

The abdominal segments gradually increase in size from the 1st, which is the smallest, to the 9th.

The *muscular impressions*, present on the abdominal segments of most Elaterid larvae, can hardly be made out in this genus; the longitudinal branch can, however, sometimes be seen behind and somewhat dorsal to the spiracle, running nearly parallel to the lateral suture.

The 9th abdominal segment is considerably longer than the preceding one, conically paraboloid (as Beling<sup>(2)</sup> aptly describes it), with a pair of large open pits, margined with brown, situated one on either side near the anterior margin of the tergite (Plate IV, fig. *a*). In life they are nearly round, but contract at the sides to an elongate oval shape when preserved in spirit. Their margin of stout brown chitin is somewhat raised above the general area of the tergite on either side. Within, the pits are lined with pale membrane, which bears numberless minute dark hairs arranged over the entire surface. Similar fine hairs are also found on the inner surface of the chitinous rim just mentioned. In consequence of the presence of these hairs situated within the pits, the latter are presumed to have a sensory function, though what it may be has not yet been ascertained. Formerly, they were wrongly supposed to be spiracles, but more recently they have been referred to as muscular impressions by Henriksen<sup>(7)</sup> and Schiödte<sup>(12)</sup>.

From the posterior margin of each of these pits an almost straight suture runs backward, terminating beyond the middle of the segment, slightly more dorsal than the sensory pit. Situated between these two sutures is another pair of parallel sutures, arising and terminating at corresponding points of the tergite (seen in Plate IV, fig. *b*).

The apex of the segment is brown and is slightly produced into a stumpy cauda.

The 9th tergite (Plate IV, fig. *a*) is continued uninterruptedly on the ventral surface for about half its length posteriorly, while the 9th sternite, which is an arch-shaped area and contains the pseudopodium near its apex, is separated from the tergite by a deep and brownish

suture. Within the suture is a belt of strong yellow chitin, marked transversely with striae similar to those forming the border to the other segments. The remainder of the sternite is a semi-ovoid area strongly chitinised and almost smooth. This encloses near its apex, posteriorly, the cylindrical pseudopodium, which is by some considered to represent the 10th segment. Surrounding the pseudopodium the 9th sternite is convex and margined with a concentric border of fine striae in a somewhat darker yellow area. The *pseudopodium* itself is white, fleshy and tubular and bears around its base a whorl of eight short, tapering, incurving hairs. It is situated somewhat anterior to the middle of the 9th abdominal segment. The anal aperture is linear and extends across the pseudopodium in the longitudinal axis.

The 9th tergite both above and beneath bears numerous rather long yellow-brown hairs, which are more numerous towards the apex. The 9th sternite, anterior to the pseudopodium, has a transverse row of six hairs, the two median ones of which are shorter and slightly anterior to the rest. A single short hair is also usually present on either side of the pseudopodium.

#### HEAD AND MOUTH-PARTS OF LARVA.

On the dorsal surface of the head there is a *cephalic plate*, expanded anteriorly over the base of each mandible, tapering posteriorly and ending in a point in the occipital region (Fig. 2a). Doubtless it is composed of several fused sclerites, probably the frons, clypeus and labrum. Laterally it is separated from the epicranial plates by a deep suture. In *Agriotes*, and apparently also in *Cardiophorus*, the *epicranial plates* meet for a short distance at the base of the head (vertex) behind the cephalic plate, though in most Elaterid larvae the apex of the cephalic plate extends backwards to the posterior margin of the head and the epicranial plates are dorsally entirely separated by it. On the ventral surface the cephalic plates are fused together posterior to the base of the hypostome and though there is little sign of a suture in the median line, there is a distinctly darker line ventral to the tentorium which probably represents the line of junction. There appears to be no true gula.

In its general plan the structure of the *tentorium* is simple. On the floor of the head at the base two arms extend for a short distance on either side, almost parallel to the thickened margin of the occiput. From the occiput the main longitudinal trunk is carried forward by two beams, closely approximate, on the floor of the head to the base of the maxillae. At this point two small plates of thickened brown chitin are developed

on the tentorium and with these plates the cardines of the maxillae articulate at their posterior apices. From this point one pair of arms extend, diverging somewhat, beneath the margins of the hypopharynx to the inner margin of the mandibles. A second pair, more dorsal, extend forwards, diverging outwardly towards the large flexor tendons of the mandibles, but terminating abruptly with a number of short ligaments before reaching them.

The *antennae* are short and are situated at the anterior angles of the head, close to the base of the mandibles. They consist of (1) a stout basal segment, nearly twice as long as broad, rounded on the outer but almost straight on the inner side, and bearing a rather long tapering seta not far from the apex on the outer margin; (2) a second segment about two-thirds the length of the first and more slender, widest near the apex and bearing a short seta on the inner side of the apex; (3) two processes at the apex of the second segment, borne separately, the ventral and shorter one conical, very thinly chitinated and nearly colourless, the dorsal and longer one more slender, yellow and strongly chitinated, about equal in length to the second segment, though not more than half as broad. The apex of the dorsal process bears a long stiff seta and also three minute ones, all projecting forward, the first-named being longer than the process itself. In Carabid and Staphylinid larvae, where somewhat similar processes are found on the antennae, Kemner<sup>(8)</sup> regards the longer process as the terminal segment and calls the shorter ventral one "supplementärglied." Gahan<sup>(6)</sup> has suggested that the latter is a sensory organ.

Three pores, which appear to have a sensory function, are present in the basal segment. In the second segment a pore bearing a short spine is present on the outer margin near the distal end, while another similar pore may be found near the middle of the anterior margin.

The *eye* is small, dark brown or black, situated laterally, a little below the base of the antenna. The chitin of the head is continued uninterruptedly over it and is not raised.

The *mandibles* are curved inwards and bear on their inner surface two denticles. The first of these, situated near the apex, is flattened dorsi-ventrally and overlaps the mandible of the opposite side when the two are brought together, that of the right mandible usually, but not invariably, overlapping the left. The presence of this denticle is characteristic of the genus *Agriotes* amongst Elaterid larvae, though it is present in certain other groups of coleopterous larvae. It is somewhat rounded in outline, though its anterior margin forms almost a right

angle with the inner edge of the mandible at the point of junction, and projects in the horizontal plane.

The second denticle, also on the inner face of the mandible, is situated nearer to the base. It is much sharper than the first and is on a plane nearer to the ventral surface of the mandible, arising from a point a little within the actual margin. This denticle is called by Schiödte the *retinaculum* and is common to all the Elaterid larvae known with the exception of the section *Agripnini* (of which *Brachylacon murinus*, L. is our only British species) and the genus *Cardiophorus*.

At the base of the inner edge of the mandible there arises a small process of brush-like structure called by Schiödte and Henriksen the *penicillus*. Ford, who gives a figure of the mandible<sup>(5)</sup>, has called this process the "lacinia mobilis," but it is certainly not homologous with the lacinia mobilis of some of the Malacostraca, to which the term was first applied. In them, as Mr L. Borradaile has kindly pointed out to me, the process is independently moveable, whereas the process in *Agriotes* is fixed. Its function seems to be to cooperate with the rest of the dense mass of hairs at the entrance to the mouth in preventing the entrance of unwholesome matter to the mouth. Schiödte, however, refers to it as assisting in the absorption of blood. Several hair follicles are visible on an examination of the dorsal surface of the mandible, of which one is situated about in a line with the retinaculum and almost on the outer margin of the mandible: two others are situated nearly in the median line, more basally. The first of these bears a seta of considerable length, which extends obliquely forwards and doubtless has a tactile function.

The mandible itself is of considerable thickness and somewhat excavate on its outer side, but is narrowed on the inner side to form the cutting margin. In transverse section it is therefore almost triangular. Much variation appears to exist in the mandibles of this species, but some of the apparent variation is caused by erosion, mandibles which should normally be sharp-pointed and somewhat long presenting an appearance of stumpy bluntness.

The principal condyle is ventral and articulates with the thickened anterior margin of the epicranial plate, ventral to the base of the antenna.

Between the mandibles, at the anterior margin of the compound structure which has been called the cephalic plate, there is a thickening of the chitin into a tridental process, of which the middle denticle is the longest (Fig. 2 b). This process is situated immediately above the entrance to the mouth and was referred to by the older writers as the clypeus, but

as it probably only represents a portion of the clypeus it is perhaps better to adopt Henriksen's term of *nasale*. This also, like the mandibles, is much subject to erosion and though the three denticles are visible as a sharply pronged trident in some specimens, in others they are worn down to a level with the base. Variation appears to take place to some extent in regard to this organ, one specimen having been found bearing four denticles.

Ventral to the "nasale," nearly apposed to it, and also extending outwardly, is another chitinous process, semi-lunar in shape and bearing

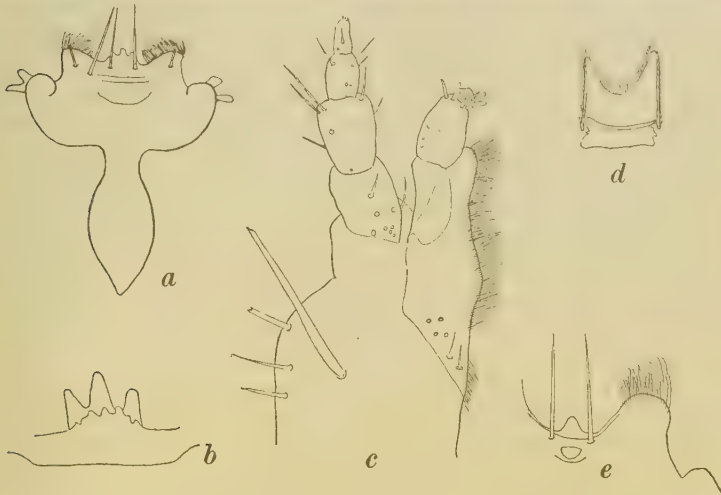


Fig. 2 a. Cephalic plate of larva.  
 b. Nasale and subnasal process from beneath.  
 c. Anterior portion of maxilla.  
 d. Hypopharynx.  
 e. Nasale of larva in first instar.

some seven teeth (Fig. 2 b). It does not extend so far as the nasale, the points of the teeth reaching little beyond the base of the nasale. The teeth are asymmetrically disposed and of unequal length. They may also, with the nasale, be supposed to provide a gripping surface in apposition to the mandibles. No suture has been found between the nasale and this process to indicate that it is a separate sclerite, though so much fusion appears to have taken place between the sclerites on the dorsal surface of the head, that it may possibly represent the labrum of other insects. A similar process has been found in the larva of *Dichiro-*

*trichus placidus*, Gyll., a Carabid, by Kemner<sup>(8)</sup>. From the base of this process the chitin is continued in a fairly thick band on the palate of the mouth.

On either side of the nasale the anterior margin of the cephalic plate bears a tuft of fine yellow hairs, screening the opening of the mouth. The aperture itself is small and of a contracted oval shape. Within the mouth, on its lower surface, the *hypopharynx* is situated (Text-fig. 2*d*). It is composed of a basal bar of stronger chitin, followed by an anterior portion, less strongly chitinised. This latter is yellow and almost quadrate in form, save for the anterior margin, which is deeply excavated in a semicircular form, leaving a slightly projecting horn at the entrance to the mouth on either side. Its surface, both dorsal and ventral, is covered with minute hairs in transverse rows. The main portion of the hypopharynx is strengthened by a rim of thicker chitin supporting its lateral margins. Its anterior margin and sides, but especially the apices of the projecting horns, bear a mass of fine yellow hairs, which doubtless perform the same function as do those constituting the penicillus of the mandible and the tufts on either side of the nasale. The apices of the horns fit up to the basal portion of the laciniae on either side, the base of the hypopharynx being slightly anterior to the base of the mandibles, but considerably posterior to the nasale. The length of the hypopharynx in a full-grown larva, measured from the exuvia, was .28 mm., the width .26 mm.<sup>1</sup>

Ventral to the hypopharynx but attached to it at the base is a semi-membranous plate, the floor of the mouth. In length it is about double that of the basal plate of the hypopharynx and therefore is considerably less than the hypopharynx itself. In breadth it extends considerably beyond the margins of the hypopharynx and near its antero-lateral margin bears a small tuft of bristles on either side in juxtaposition to those of the anterior margin of the cephalic plate just referred to. The anterior margin is somewhat bowed inwards and is bordered by minute hairs. Ventrally and almost on a level with the side margins of the hypopharynx on either side is a brownish semicircular mark, with five or six alveoli, which may be sensoria, situated in two rows on its anterior border.

<sup>1</sup> Miss A. M. Evans in a recent paper on the hypopharynx and maxillulae (*Journ. Linn. Soc.* 34 (1921), 429-456) figures the hypopharynx of the larva of *Campylus linearis* as representative of Elaterid larvae. She considers the anterior portions which I have called "horns of the hypopharynx" to be vestigial maxillulae. In the absence of more evidence than is at present available, I have some doubt in accepting this homology and therefore retain the term used above.

On the ventral surface of the head, bounded on either side by the epicranial plates, the oval *hypostome* is found (Text-fig. 1). It projects forward much beyond the opening of the mouth and is composed of the sclerites of the first and second maxillae. Around its margin, forming the boundary of the maxillary stipites, there is a rim of stouter chitin, corresponding to a similar but even stouter rim at the margin of the epicranial plates. The latter originates close to the point of articulation of the maxillary cardo with the tentorium and reaches almost to the base of the mandibles on either side, gradually becoming more slender as it extends forwards.

Between the two rims of thickened chitin there is a considerable flap of membrane which is ordinarily tucked in between them. At the base of the hypostome, posterior to the submentum and maxillary stipites, there is a considerable field which, save for the two pairs of small sclerites which constitute the cardines, is also membranous. The hypostome is thus capable of considerable extension either in the dorsi-ventral plane or simply forwards, the membranous margin causing it to function as a kind of pouch.

On either side of the hypostome, within the margins of the epicranial plates, there is a long oblique suture of a brownish colour, extending backwards from the base of the mandibles.

The two pairs of small sclerites mentioned above are situated near the base of the maxillary stipites. Each one of the outer pair, which is nearly apposed to the stipes, is of an irregular elongate form with its apex pointing obliquely backwards. Posteriorly it is attached to the tentorium at the second branch of the latter. The innermost pair of sclerites, each of which is nearly circular, is situated near the median line and sometimes overlaps the outer pair, the latter being somewhat beneath the general surface of the cuticle. Henriksen (p. 280) considers these small sclerites to have no importance and says that the outer one is not attached to the tentorium. As I have found it to be so attached, it must be considered to represent the maxillary *cardo*, as Ford has described it. No attempt can be made here to homologise the round sclerite. The outer margin of the *stipes* is rounded, the inner (bordering on the submentum) straight. It is yellow in colour, strongly chitinised and bears at its exterior angle, near the base of the palpiger, two longer and two shorter setae (Fig. 2c).

The *maxillary palps* are composed of four segments, which gradually contract in width from the basal to the apical segment. They are brownish-yellow in colour and are borne on a whitish palpiger which generally

protrudes considerably from the anterior margin of the stipes. The second segment is longer than any of the others, though not so broad as the first. Two short setae are borne on the first segment, a whorl of four around the apex and two at the outer margin of the second, a similar whorl of four near the apex of the third, and two very short ones near the middle of the fourth. At the apex a series of ten or more exceedingly minute short bristles are present, which must make the palps extremely efficient tactile organs. In addition to the setae a number of pores are present on the palps, of about the same size as the follicles of the setae. These have presumably a sensory function and occur as follows:

Segment 1; a single pore at the base, in the median line of the ventral surface, also a cluster of six pores of varying size near the inner margin: segment 2; one large pore somewhat beyond the middle of the segment and one very small one at its base, both on the ventral surface: segment 3; two pores placed side by side on the ventral surface near the middle of the segment: segment 4; one pore on the outer margin of the segment near its base.

The *galeae* are two-jointed, the first segment being slightly longer than the second. Its outer margin is almost straight, while the inner margin is bowed outwards, almost elbowed. It is without setae and sensory pits. The second segment is rounded at the margin on either side, but the outer is longer than the inner side and the galea inclined inwards by reason of the manner of the articulation of the first with the second segment. A large sensorium is borne near the middle of the segment on the ventral surface, while four or five smaller ones are borne on the outer margin between the middle and the base. The apex of the segment is surrounded by a whorl of six short thick setae and within the whorl a colourless thimble-shaped process is enclosed. This process is inclined inwards and is barely one quarter the length of the preceding segment. It is covered with rounded, colourless scales.

The *lacinia* lies somewhat dorsal to the galea and is partially overlapped by it. It is flattened, composed of a single segment with the apex bluntly pointed, almost triangular and reaching a little beyond the first segment of the galea. On its outer margin it articulates behind (*i.e.* dorsally to) the base of the galea, while its inner margin is continued posteriorly to a level with the opening of the mouth, at the base of the terminal lobe of the labium. The whole inner margin and apex is almost concealed by a dense mass of wavy yellow hairs, which arise for the most part near the outer margin of the organ and protrude into the space before the mouth. At the base, near the angle of the inner margin two

short setae are situated and above them eight or nine pores of varying size.

The *submentum*, which constitutes the basal piece of the labium, is strongly chitinated, elongate with parallel sides and the base bluntly pointed. It extends from a point level with the bases of the maxillary stipites to the point of insertion of the lacinia. Its anterior margin is almost straight and it bears four long tapered setae in pairs at its anterior and posterior angles. Many small pores are found on the surface.

The *mentum* is membranous, nearly colourless, transverse and joined at its sides for about half the length to the inner margins of the laciniae. The anterior half is free. It is joined to the submentum just posterior to the level of the insertion of the laciniae and is produced forwards nearly to the level of the insertion of the galeae. The mentum is broader than the base of the *terminal lobe* of the *labium* which succeeds it but the angles are rounded off.

The terminal lobe itself, composed of the fused palpigers and ligula, is nearly pentagonal in shape. The labial palps are situated one on either side of the anterior margin, while between them the margin protrudes forwards a little in a pale rounded projection, which is evidently the ligula. Further back the palpigers may generally be roughly traced by the darker colour of the cuticle on either side, that overlying the ligula being pale and extending almost to the base of the apical lobe.

A pair of setae are situated dorsally near the apex of the ligula, projecting forwards and a second pair occur ventrally a little posterior to the first. The longest pair are placed one on each palpiger at some distance from the base of the palp, while a fourth pair of quite short spines are found not far from the base of each palpiger.

In addition to the setae there are a number of pores on the ventral surface of palpigers and ligula, as follows: a row of three between the two long setae of the palpigers, a single unpaired one on the left side just behind them, and a pair behind the setae, followed by a single unpaired median pore, while yet another pair occur almost in a line with the short basal spines, one on the outer side of each. All these pores appear to have a rather wide rounded margin with only a very minute aperture (or perhaps a sensory pin) in the middle.

The *labial palps* are each composed of two segments. The basal segment is stout and considerably rounded at the sides, especially on the inner side. It is yellowish like the general surface of the cuticle, but is paler at the apex. The apical segment is only about half the breadth of the basal segment, brownish yellow, slightly turned inwards and gradually

narrowed to the bluntly pointed apex. A pore, probably sensory, is situated near the base of the segment, while a second, bearing a short spine is present near the middle. The apex, like that of the maxillary palp, has an exceedingly minute tuft of short spines, which just break the surface of the cuticle and are visible only under the microscope.

In the basal segment there is a whorl of four moderately long setae near the apex, two of these being ventral, the others dorsal. Two pores are situated near the inner margin of the segment, one behind the other, a third in the median line near the base, and a group of two or three pores near the base of the outer margin.

The pores found on the palps appear to be more open than those on the body of the labium.

#### SPIRACLES OF LARVA.

The two thoracic spiracles are situated in the pleurae of the mesothorax. They are larger than those of the abdominal segments but are otherwise similar in structure. They lie almost, if not quite, parallel to the longitudinal axis of the larva.

The abdominal spiracles, which are present in each of the abdominal segments 1 to 8, are placed in the anterior third of the dorsal scutum on either side, just above the longitudinal groove separating the tergite from the epipleura. In their case the long axis of the spiracle does not lie parallel to that of the long axis of the larva but is raised anteriorly so as to form an angle of some 45 degrees.

The shape of the complete spiracle is elongate oval (Plate IV, fig. *d*) and it is broader in proportion to its length in *A. obscurus* than in *A. sputator*. Each spiracle is provided with two slit-like orifices, between which there is a wide septum, widest at the surface (Figs. 3*a*, 3*b*). The septum divides the spiracle completely into two chambers and is continued anteriorly beneath the cuticle. In this portion of the spiracle, which I have named the antechamber, there are a number of pale coloured processes or trabeculae, sometimes branched, which extend far across the lumen of each antechamber. Internally another chamber called the atrium (see Böving(3)) comes into apposition with the antechambers and receives the air from them (Fig. 3*b*). It is not, however, so wide as the width of the two antechambers and the latter are continued a little beyond the opening of the atrium, leaving a slight *cul-de-sac* in each case. From the antechambers the atrium extends inwards (*i.e.* away from the cuticle) for a distance of about double its width to meet the trachea which carries the air thence to the main longitudinal trachea

on either side of the body of the larva. At the point of contact of the atrium and the trachea there is a slight thickening around the latter.

There are no taenidia lining the atrium, but its epithelium is composed of irregular pentagonal cells, which are plainly visible in a stained preparation, even of an exuvia. Miall and Denny<sup>(10)</sup> have described a very similar chamber with polygonal epithelial cells as existing just within the stigmatic orifices of cockroaches and Böving<sup>(3)</sup> has described it in the larvae of *Donacia*, *Hister* and an Elaterid from Java.

The margins of the two stigmatic orifices are thickened into a peritreme of stout brown chitin, the surface of which, as well as the sides and

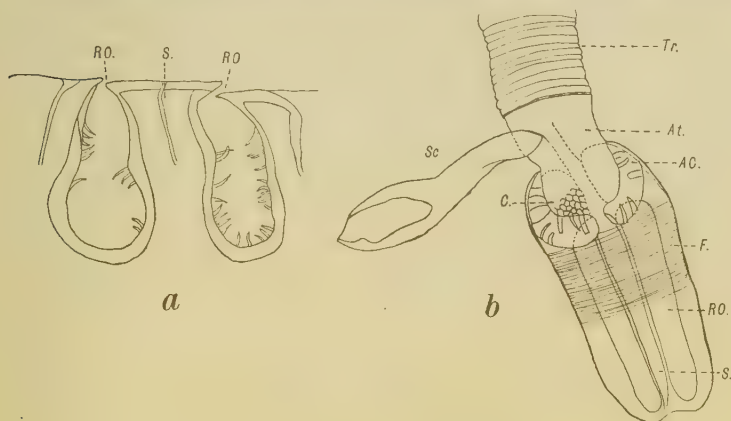


Fig. 3 a. Transverse section of larval spiracle.

b. Larval spiracle as seen from beneath.

Sc.=Scar; S.=Septum; RO.=Respiratory orifice; F.=Floor of spiracle; AC.=Antechamber; At.=atrium; Tr.=Trachea; C.=polygonal cells of atrium (a few only shown).

floor of the orifice itself, is transversely corrugated. A fine, somewhat irregular, suture separates the peritreme of each orifice on the surface of the septum. At the anterior and posterior ends of the orifice, the peritreme is narrower, especially at the posterior end. In young larvae of the first and second instars the peritreme is invisible at the anterior end, though present as a narrow ridge of chitin at the posterior end.

The corrugations already mentioned which project as small teeth on either side of the stigmatic orifices, vary in number according to the instar. In the final instar they number some 47 in the thoracic and 40-43 in the abdominal spiracles. In the young larva of the first instar they

number only about seven to eight in the thoracic and five to six in the abdominal spiracles.

Towards the anterior end of the atrium there is attached an apparent strut, connecting the atrium with the outer cuticle near the anterior end of the spiracle but a little more dorsal and running at right angles to the axis of the spiracle. This "strut" is moulted with the exuvia. It is not present in the first larval instar, although present in the second and subsequent ones. Evidently it is the scar left by the withdrawal of the trachea at the last preceding ecdysis, as was pointed out by Schiödte<sup>(12)</sup>, at p. 493). At the point where the trachea has been withdrawn through the cuticle there is an oval scar of a brownish colour at the margin and sometimes bearing a septum of similar colour through its long axis. The central area of this scar is covered with yellow chitin, similar to the general colour of the cuticle and was evidently deposited subsequently to the withdrawal of the trachea.

At ecdysis the position of the spiracle is moved back a little and the lining of the atrium, with a considerable length of tracheal lining from beyond it, comes away with the exuvia, leaving the scar in the body of the newly moulted larva anterior to the new spiracle. This moving back of the spiracle at each ecdysis does not however imply any change in its position in each instar relative to the other parts of the body, as measurements have shown. The extent of the change of position therefore merely corresponds to the increase in growth of the larva.

The necessity for some provision to avoid the difficulty of extracting whole a tracheal tube through a biforous stigmatic opening is manifest. This phenomenon of the growth of a completely new spiracle, alongside the old, appears to resolve the difficulty.

De Meijere<sup>(9)</sup> found somewhat similar remnants of spiracles in the case of amphipneustic dipterous larvae, although in the cases dealt with by him the cause was apparently the covering of the stigmatic orifice by a membrane, usually complicated, which could scarcely be renewed after ecdysis had taken place.

Böving<sup>(3)</sup> deals with the anatomy and functions of biforous spiracles in coleopterous larvae and speaks of a "spiracular slit" near the spiracle in *Hister*, which he figures, as well as sections of the spiracles of a larval Elaterid from Java. In neither of these cases do his sections show the "spiracular slit" completely closed, but probably in both cases it represents the scar of the trachea just described.

Scott<sup>(13)</sup> found biforous spiracles of very similar structure in the larva of *Epuraea depressa*, but he does not describe any scar.

Not infrequently larvae are found having one or more "blind"

spiracles with no opening to the exterior but merely a brown spot of hardened chitin indicating the position of the atrophied spiracle. Probably a functional spiracle would reappear after the next ecdysis, but no investigations into this subject have been made.

#### PUPA.

The pupa has been described by Curtis(4), Beling(2), Ford(5) and others. A few notes on certain points which require amplification are therefore all that it seems necessary to add.

At the base of the pronotum on either side of the median suture a small papilla is placed. These do not bear spines. Nine abdominal segments are visible, the external genitalia being seen in their pupal sheaths in apposition to the ventral surface of the ninth.

In the male, close to the margin of the 8th sternite, there is a rounded and slightly notched flap, which probably represents the 8th sternite of the adult. Posterior to this flap and arising from beneath it are three rounded lobes, the median one not extending so far posteriorly as those on either side of it. Probably these represent the median and lateral lobes of the male external genital organs (Fig. 4*a*).

In the female (which was the sex described by Ford) the 8th sternite is slightly produced into a blunt point behind and bears two small punctures side by side near the apex. From beneath the 8th sternite the pupal sheath of the ovipositor arises. This is elongate, subparallel and has a deep suture in the median line. At each of the posterior angles there is a small pointed papilla, which is the sheath of the tactile process at the apex of the ovipositor.

The apex of the ovipositor is almost co-terminous with that of the 9th tergite (Fig. 4*b*). The small spurs observed by Ford (p. 108) at the base of each posterior spine, though frequently present, are not constant and are sometimes present on one side only. Ancillary unpaired spines may also occur on the cerci or even on the median posterior portion of the segment.

In both sexes the sternite of the 7th abdominal segment is produced posteriorly, so as partly to cover the next segment. In the adult the 7th is the last visible segment and the sternite is similarly produced to a blunt point posteriorly. The preceding sternites (2-6) of the pupa have their anterior and posterior margins subparallel as in sternites 3-6 of the beetle. The 1st sternite is very narrow and is represented by a mere fold of the integument. Both tergites and sternites of the 2nd to the 8th abdominal segments are produced laterally a little at the posterior margin, but not so much as to conceal the spiracles.

The apex of the elytral sheath is slightly hooked but less so than in some allied species (e.g. *Athous haemorrhoidalis*). The number of spiracles is the same in the pupa as in the larva. The single thoracic pair is situated ventrally in the membrane between the pro- and meso-thoracic segments, anterior to the intermediate coxae. The abdominal spiracles are situated laterally in the pleurae between the folds of the tergite and sternite, but are not concealed as in *A. sputator*. Those of the first segment are almost in the middle of each pleura, the remainder, on segments 2 to 8, are near the anterior margin of the pleura.

The spiracles are uni-forous, almost circular and bear on their

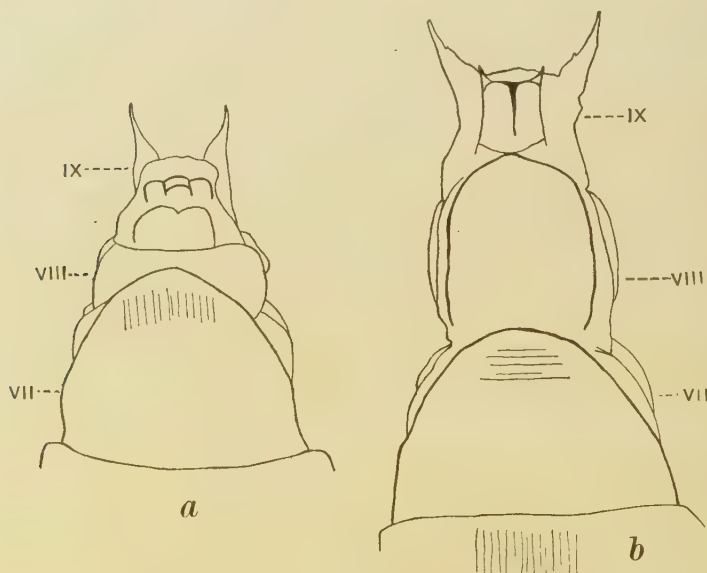
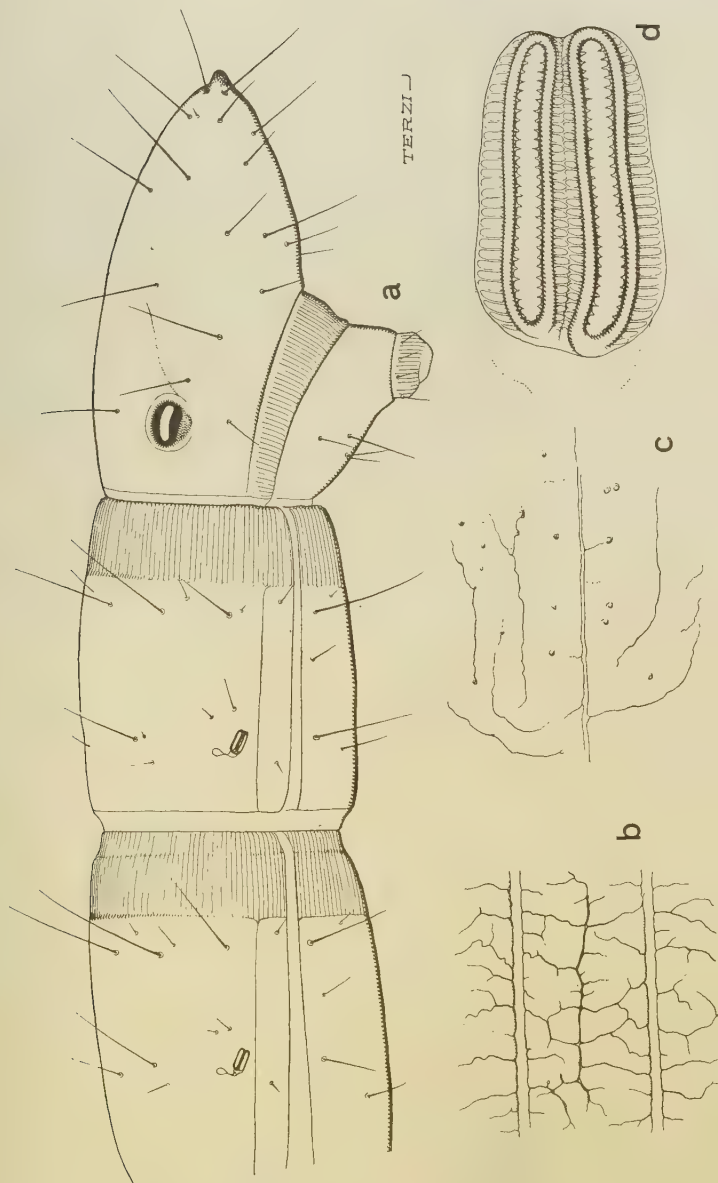


Fig. 4. Terminal segments (a) of ♂ pupa, (b) of ♀ pupa, from ventral surface.

posterior margin somewhat dorsally a small round scar with a fine linear cicatrix in the middle. There is no appearance of any atrium and the taenidia extend to the aperture.

It is interesting to compare the segments and spiracles of the pupa with those of the adult. In the latter there is one pair of spiracles more than in the pupa or larva. There are the same number (eight) in the abdomen, but two pairs in the thorax, situated (1) ventrally, in the membrane between the pro- and meso-thoracic sternites, on either side of the prosternal process and (2) dorsally, in the pleurae of the meta-thorax, beneath the insertion of the wings.





Again, in the abdomen of the adult beetle there are normally visible seven tergites dorsally and but five sternites ventrally, the first two sternites being suppressed beneath the third. Within the 7th segment the 8th is concealed for the greater part of its length. In the female the ovipositor arises from this segment and in the male there are evidences of two rudimentary segments beyond it, as Verhoeff found<sup>(15)</sup>, making ten in all. Stein<sup>(14)</sup> made out nine abdominal segments in the female, considering the ovipositor to be formed of the 9th tergite and 8th and 9th sternites. The eighth, however, is the last segment bearing a pair of spiracles in both sexes, so that the remaining two segments, if true segments, must constitute parts of the ovipositor. The "Vaginal palpe," or tactile process on either side of the aperture of the oviduct, is the terminal one according to Stein.

Therefore though there is considerable similarity between the form of the first seven abdominal segments in the pupa and the adult, the segments posterior to the 7th are entirely different, continuing to taper gently to the apex of the 9th in the pupa, while in the adult they are much narrowed and normally contracted within the body of the beetle.

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## EXPLANATION OF PLATE IV

*Agriotes obscurus*, L. larva in late stage.

- a. Last three segments.
- b. Cuticle of 9th abdominal segment, between the sensory pits (much enlarged).
- c. Cuticle of 8th abdominal segment along the medio-dorsal suture (much enlarged).
- d. Spiracle.

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NOTE ON THE CHEMOTROPISM OF THE  
HOUSE FLY

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THE following notes have been called forth by the perusal of two recent papers in this *Journal*, viz. those by Imms and Husain (1920) and by Speyer (1920). The observations were made mainly at Aboukir, on the north coast of Egypt between 1916 and 1919. As may be imagined, the aim in view was the destruction of the flies, and the haphazard experiments were carried out in addition to much other work and with no thought of publication. They, however, appear to confirm the observations of the above-mentioned investigators by trials on a large scale.

It was found that formalin, when dilute, was at times very effective if exposed in a shallow dish near a window. The presence of a little bread or something to give the flies an alighting ground increased its usefulness. Flies apparently drink in the morning<sup>1</sup>, as early as possible, and for this reason the formalin should be available at that time. When allowed to stand in the light, formaldehyde changes into one of its solid polymers, as may be noticed when the solution evaporates. The latter, however, appears to be poisonous to flies, though no direct observations were made on this point, a little formalin always being present. As pointed out by Morrill (1914) the behaviour of formalin in attracting flies is very variable. If too strong they appear to be driven away and in the presence of miscellaneous foodstuffs they will usually leave a formalin solution untouched.

As noted by other observers, beer is a very attractive substance to flies. It was found that dome-shaped glass vessels with a rim turned up inwards made excellent traps when the annular trough was filled with beer. The domes were supported on three legs and placed for preference in the sun or a well-lighted position. The number of flies caught in such traps within two hours of their first being tried at Aboukir was quite amazing. These traps were not, however, available in any quantity, nor were the Japanese clockwork traps, so attempts were made to render weak formalin more attractive by adding cane sugar, also

<sup>1</sup> The water supply of the numerous beetles inhabiting the patches of baked clay in the coastal deserts was a puzzle to the writer till it was noticed that they drank drops of dew from the angles of dried-up thorny plants.

ethyl alcohol. Beer, however, was much better as a lure, and it was also noticed that the addition of a little Egyptian made alcohol was very effective. Dishes containing about 1 per cent. formalin and a little of this crude alcohol compassed the death of many thousands of flies in our camp. Doubtless the amyl alcohol, of which, together with the other fusel oil constituents there appeared to be a noticeable amount in this product, attracted the flies, and some traces of esters of these alcohols may also have been present.

Speyer has drawn attention to the attraction that iso-amyl acetate and other esters of these alcohols have for flies. There is no doubt that it is very powerful, for our "doping" sheds were usually infested with flies even when neighbouring sheds or hangars were comparatively free from them. Now aeroplane "dope" consists of acetyl cellulose dissolved in a mixture containing acetone, methyl-acetate, methyl alcohol, ethyl alcohol and benzene as solvents or diluents and benzyl alcohol as a residual solvent to keep the film pliable. Though neither benzene, acetone, methyl nor ethyl alcohol attract flies in any noticeable manner, the methyl acetate may have a decided positive effect, and it is just possible that benzyl alcohol may also, but this is rather unlikely, as shown by Speyer.

Far greater however than the attraction of dope was that exerted by the nitro-cellulose varnish, in which the main solvent was iso-amyl acetate at first, and later on *n*-butyl acetate, the *n*-butyl alcohol having become available as a result of the preparation of acetone by a bacterial process. The thousands of flies attracted from a neighbouring village by the strong odour of butyl acetate afforded an example of chemotropism on a very large scale.

The considerable supplies of *n*-butyl alcohol produced in the preparation of acetone by the fermentation method have resulted in this alcohol becoming available in surplus, so its utilization in quantity as the acetate in a campaign against flies ought to be possible. The ester is volatile, and boils at 125° C., so it would have to be replenished at intervals. Iso-amyl acetate is slightly less volatile and boils at 139° C.

#### LITERATURE CITED.

- IMMS, A. D., and HUSAIN, M. A. (1920). Field experiments on the chemotropic responses of insects. *Ann. App. Biol.* vi, 269-92.  
MOBRILL, A. W. (1914). Experiments with house-fly baits and poisons. *Journ. Econ. Entom.* vii, 268-74.  
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## REVIEW

*Annales du Service des Épiphyties*. Edited by MARCHAL, P. and FOEX, E., Tome VI, pp. 1-365. Mémoires et Rapports présentés au Comité des Épiphyties en 1918. Ministère de l'agriculture, Paris, 1919.

The above volume contains much useful information regarding investigations carried out in France on insect pests and fungoid diseases of plants.

A brief report on Phytopathology in France for the year 1918 introduces the volume (pp. 1-33), and reports on the activities at the various entomological and vegetable pathology laboratories in France occupy the concluding pages.

Of the papers on entomological investigations, Professor F. Picard, Professor of Zoology at the National School of Agriculture at Montpellier, gives an exhaustive study of the entomological fauna of the fig-tree, pp. 34-174. The paper is divided into two sections, I, Special part; II, General part.

The first part deals with the more important insects which attack the wood, the leaves and the fruit respectively. Description of the insects, ample biological notes, their enemies and parasites are given.

Only one species of Lepidoptera (*Simaethis nemorana* Hubn.) frequents the fig tree in France, a fact which is discussed in Part II of the paper.

Part II consists of a general discussion on the relation of plants to insect population. The views expressed are largely formed from extensive observations on certain insects associated with cultivated plants, especially with regard to the fig tree and exotic plants in general. The question of the introduction of pests into new countries and the reasons for their subsequent wide distribution, are discussed.

Certain species of plants are populated by many species of insects, while others may only support one or two species. Chemotropic influence of the odours of plants, probably is the most important factor concerned. The significance of physical factors such as light, temperature, humidity etc. are discussed in relation to the insect population of plants.

The factors which are at work in keeping down insect pests are numerous and complex in their inter-relationship. Parasites, epidemic diseases, birds, and climatic conditions all play their part.

Cultivation carries with it a great quantitative and qualitative modification of the fauna of plants. A chapter is given on the relations between the parasites of insects and their hosts.

Professor P. Marchal gives an account of arsenical sprays and the treatment of fruit trees in America and France, pp. 242-280.

A section is devoted to the relation of arsenical sprays to the consumer of fruit. The results of experiments quoted, show that owing to rain and atmospheric conditions generally, the danger is negligible. Obvious precaution is necessary after spraying with regard to cattle and herbs which grow in orchards. Observations and recommendations based on experiments carried out in 1917 are given and an extensive bibliography is appended.

Among the mycological papers Professor E. Foex, Director of the Vegetable Pathology Station in Paris, gives detailed observations of *Leptosphaeria herpotrichoides*, the causative organism of a disease of wheat, pp. 200-213. The practical application of the results of the investigations are summarized.

Professor L. Ravaz, Professor at the National School of Agriculture, Montpellier, in an account of experimental research on the treatment of vine mildew, pp. 281-288, gives much useful information of practical value, especially with regard to the effect of spraying formulae on the plant and on the fungus.

G. Arnaud has given notes and descriptions of some new or little known diseases in France. The author notes the development of *Rhizoctonia solani* on potatoes, due to the favourable dry season, while on the other hand *Phytophthora* has been greatly restricted.

An interesting article on the destructive action of fumes from the Chedde factory in Savoy is written by Professor L. Mangin, pp. 187-199. The author shows that *Hydrochloric* acid, which are the harmful fumes, exerts the greatest effect during foggy weather, and least during dry periods.

Several other mycological and entomological articles complete this most interesting and valuable volume.

J. D.

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